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The Canadian Entomologist

VOLUME XCII MAY 1960 NUMBER 5

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The Canadian Entomologist

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External Anatomy of the Adult of *Hylobius warreni* Wood (Coleoptera: Curculionidae) and Comparison with *H. pinicola* (Couper)[1]

By G. L. Warren[2]

Introduction

There are five known species of the genus *Hylobius* in North America. These are *H. congener* Dalla Torre, Schenkling and Marshall, *H. pales* (Herbst), *H. radicis* Buchanan, *H. pinicola* (Couper) and *H. warreni* Wood. Buchanan (1934) recognized the first three species and indicated that "there might be one or two additional races or species". He also stated, "*Hypomolyx piceus* Deg. is placed in *Hylobius* in the Junk catalog; it differs from the above 3 in its untoothed femora." Wood (1957) recognized *H. pinicola* (Couper), invalidated the generic name *Hypomolyx*, and erected a new species, *Hylobius warreni*. He briefly described the new species and presented a taxonomic key by which it could be distinguished from *H. pinicola* and a Eurasian species, *H. piceus* (DeGeer). It is now clear that *Hypomolyx piceus* as referred to by Warren (1956a, 1956b) actually consisted of two species, *Hylobius pinicola* and *H. warreni*.

The species of *Hylobius* of greatest economic importance in Canada are *H. pales*, *H. radicis*, *H. pinicola* and *H. warreni*. The larvae of these attack the root systems of coniferous trees. The first two species attack various members of the genus *Pinus* when the trees occur in light, sandy soils on relatively dry sites. The other two species attack most coniferous trees, including members of the genera *Pinus*, *Picea*, *Abies* and *Larix*, when they occur on moist to wet sites. *H. pinicola* and *H. warreni* also differ from *H. pales* and *H. radicis* in general form and structure. The two former species are larger and more robust, and lack the extensive development of the femoral spurs found in the two latter species.

Because of their similarity of structure and habits and increasing economic prominence, it is appropriate to describe one of the species of the genus *Hylobius* in detail. *H. warreni* was chosen for this study because the author is investigating some aspects of its biology, and studying the relationships between this species and *H. pinicola*. The latter is considered more primitive because it has fully developed hind wings. This characteristic is useful in applying certain morphological principles required to determine anatomical characteristics of the more highly specialized *H. warreni*.

General Appearance

The adults (Fig. 1) are large, robust, subcylindrical, elongate weevils. The males vary in length from 11.7 to 14.4 mm. and females from 12.0 to 15.1 mm. These measurements are taken from Wood (1957) who had access to a large number of specimens of wide geographic origin. Both sexes are reddish-brown, becoming darker with age. They are coarsely sculptured and sparsely clothed with white to pale-yellow hairs and slender scales that form irregular pale-yellow patches on the elytra. As the adults become older many of the scales break off,

[1]Contribution No. 614, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

[2]Forest Biology Laboratory, Winnipeg, Manitoba.

causing the integument to appear glabrous. The pronotum is irregular in outline and roughly sculptured, usually having a slight mesal carina outlined by slight depressions (Fig. 2, Ca). Each elytron has 10 punctate striae, which converge caudad to a poorly defined apical umbone.

There are no reliable secondary characteristics that may be used to distinguish the sex of living specimens of this species. According to Wood (1957), "the head, thorax and elytra are indistinctly more finely sculptured, rostrum a little more slender, in the female than in the male". However, these characteristics are relative and variable and therefore cannot be used to determine the sex of a single individual. The only reliable method is the examination of the genitalia. The sex of dead specimens may be determined by removing an elytron. This discloses seven tergites in the female and eight in the male (Figs. 6, 7). The eighth tergite of the female is actually present but is concealed by the seventh.

Head

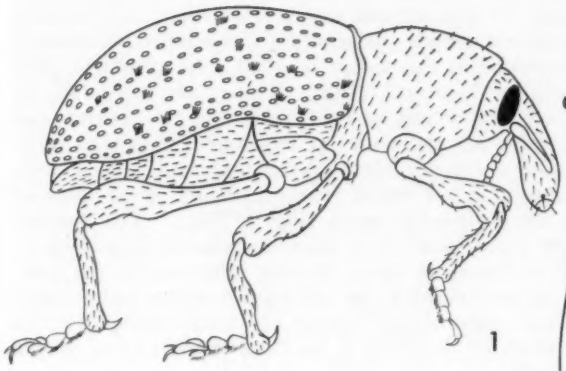
The head (Fig. 1) is produced ventrally to form a long rostrum, which widens distally. It is coarsely punctate and clothed with fine yellowish-white setae.

Since the component parts of the highly sclerotized cranial capsule lack facial sutures, the definitive areas of the hypothetical insect head cannot be separated with certainty. However, some apparently secondary features are used to assign approximate boundaries to these areas. The coronal suture is absent, as are the frontal sutures, but a deep pit or fovea occurs between the compound eyes (Fig. 9, Fo). This fovea may represent the junction of the arms of the Y-shaped epicranial suture of many insects, including the larva of this species. If this hypothesis is correct, the pit marks the dorsal limit of the frons (Fig. 9, Fr), as defined by Snodgrass (1935). According to DuPorte (1946) the frons is separated from the genae and postgenae by the frontogenal sulci, which always contain the anterior tentorial pits. These pits are absent in *H. warreni*, suggesting that the sulci are absent. However, the face contains two long antennal grooves (Fig. 9, Atg) extending distally from the eyes to the epistomal area (Es) and terminating with the antennal sockets (Ats). These grooves occupy the position normally assumed by the frontogenal sulci. They appear to be secondary structures that function as receptacles for the antennae when these appendages are at rest, and are the only facial structures that can be used to separate the frontal area from the gena and postgena (Fig. 9, Atg, Fr, Pge).

There are no sutures in the epistomal area of the face (Fig. 9, Es) separating the frons from the clypeus or indicating the presence of a labrum. The epistoma is bilobate and terminates with a strong inflection of the integument (Fig. 12). The preoral epipharynx (Ephy) is continuous with the epistomal inflection. It is weakly lobed and contains a few minute setae. There are two small groups of bristles on the epistoma; one group (Fig. 9, a) occurs just above the dorsal mandibular articulation and the other (b) above the ventral mandibular articulation.

All figures refer to *H. warreni* unless otherwise indicated.

Figs. 1-7, general outline. 1-5, dorsal and lateral outline; 3, 5, *H. pinicola;* 6, female, eighth tergite shown extended; 7, last three abdominal tergites of male. Au, apical umbone; Ba, basalare; Ca, mesal carina; Cm, costal margin; Cx, coxa; Eps, anepisternum; eps, katepisternum; Epm, epimeron; epm, postepimeron; Hp, abdominal hypopleurite; md, muscle disc; Meso-n, mesonotum; Meta-n, metanotum; Pra, prealar arm; Pro-n, pronotum; Sa, subalare; Scl, scutellum; Sm, sutural margin; Sp, spiracle (I-VIII, abdominal); St, thoracic sternum; Stn, abdominal sternite; T, abdominal tergite; Wp, wing process.



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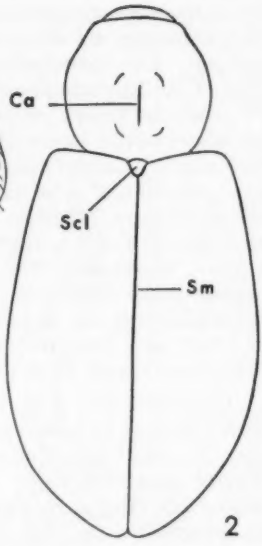
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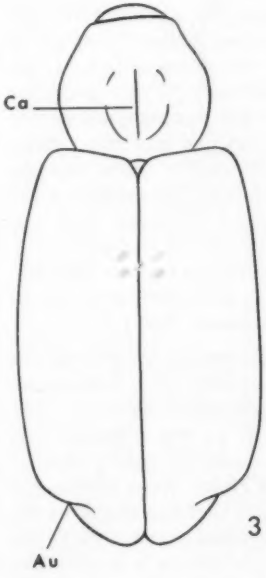
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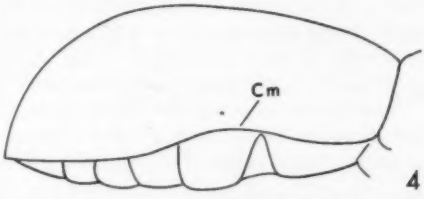
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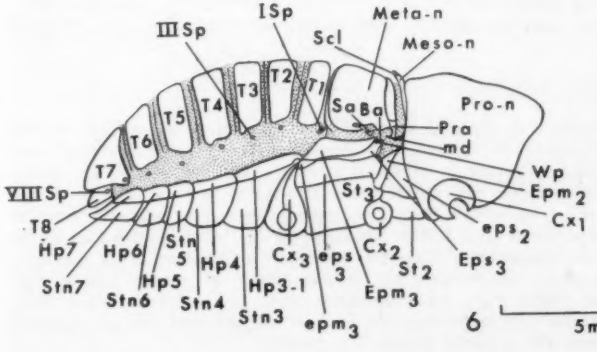
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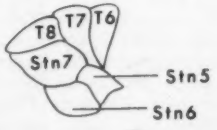
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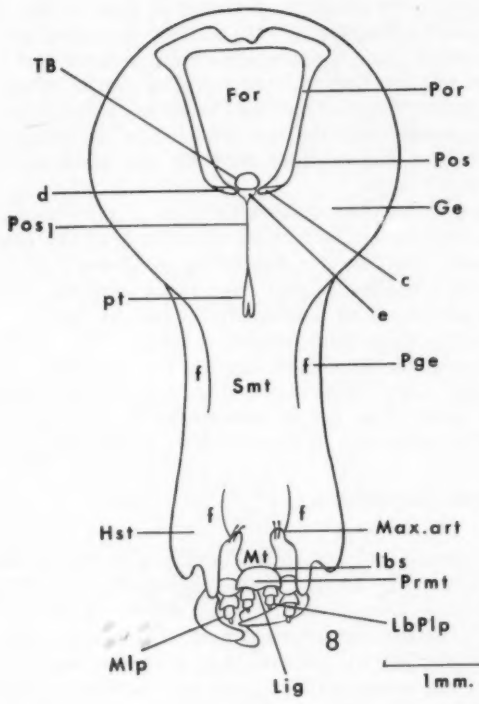
Posteriorly the head has a large triangular occipital foramen (Fig. 8, For). The foramen is surrounded by the postoccipital suture (Pos), the ventral ends of which converge and are produced distally, terminating at the posterior tentorial pits (pt). The converged portion of this suture is called, "the confluent gular suture of the Rhynchophora", by Comstock (1948). This terminology does not agree with the theory proposed by Snodgrass (1928) wherein he contends that "the postoccipital suture always has the posterior tentorial pits located in its lower ends". Careful examination of this insect reveals that the so-called "confluent gular suture" is an apparent suture caused by the infolding of the posterior wall of the head, distad to the occipital foramen (Fig. 8, Pos_1). The infolded wall (Fig. 10, Por_1) is really a continuation of the postoccipital ridge (Figs. 8, 10, Por), which according to Snodgrass is an internal inflection of the postoccipital suture (Pos). It can be conceded that this portion of the postoccipital ridge underlying the so-called "gular suture" forms a gular apodeme (Fig. 10, Por_1) but not a true gula, which by definition is the floor of the ventral part of the head and throat of an insect.

The tentorium (Fig. 10) differs considerably from the generalized type which is formed by cuticular invaginations of the anterior and pospterior tentorial arms. In this insect the tentorium is formed from the invagination of the posterior arms (Pt) only. These arms are marked externally by the posterior tentorial pits (Fig. 8, pt), which lie in the lower ends of the postoccipital suture. The posterior arms (Fig. 10, Pt) are confluent with the pits and the central corporotentorium (Ct), which forms the floor of the tentorium. The anterior arms are vestigial, being represented by a pair of spurs (At) on the margin of the bridge (TB), which is well developed. The dorsal arms (Dt) are long and slender, being attached to the inner wall of the face above and between the compound eyes. The dorsal arms are produced from the central corporotentorium and are not invaginations from the wall of the face. The tentorium is confluent with the large postoccipital ridge (Por) and the gular apodeme (Por_1).

The labium (Fig. 8) includes the mesal portion of the posterior aspect of the rostrum distad from the posterior tentorial pits. It is divided into three areas; the submentum (Smt), the mentum (Mt), and the prementum (Prmt). The large proximal submentum (Smt) is produced distally to the mentum and separated from the postgenae laterally by two discontinuous secondary sutures (f). Although it is not separated from the submentum (Smt) by a suture, the mentum (Mt) is considered to be that area of the labium that lies distad to the maxillary articulations (Max. art) and proximad to the labial suture (lbs). Its integument is smooth and glabrous whereas that of the submentum is heavily pitted and setaceous. The prementum (Prmt) is separated from the mentum (Mt) by the labial suture (lbs) and terminates with a pair of three-segmented labial palpi (LbPlp).

Figs. 8-12, head *H. warreni*. 8, occipital aspect; 9, frontal aspect; 10, sagittal section; 11, eye; 12, epipharynx. a, epistomal bristles; An, antennifer; At, anterior tentorial arm; Atg, antennal groove; Ats, antennal socket; b, epistomal bristles; c, cervical sclerite; Ct, central corporotentorium; d, cervical sclerite; Dt, dorsal tentorial arm; e, cervical sclerite; Ephy, epipharynx; Es, epistomal area; f, secondary suture; Fo, frontal fovea; For, occipital foramen; Fr, frons; Ge, gena; Hst, hypostomal area; LbPlp, labial palpus; lbs, labial suture; Lig, ligula; Mand. art., dorsal mandibular articulation; Max. art., maxillary articulation; Mlp, maxillary palpus; Mt, mentum; Od, ocular diaphragm; Or, ocular ridge; os, ocular suture; Pge, postgena; Por, postoccipital ridge; Por_1, gular apodeme; Pos, postoccipital suture; Pos_1, postoccipital suture (gular suture); Prmt, prementum; Pt, posterior tentorial arm; pt, posterior tentorial pit; Smt, submentum; TB, tentorial bridge; Vx, vertex.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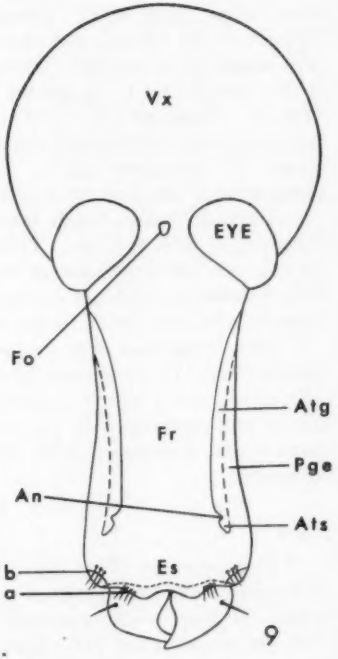
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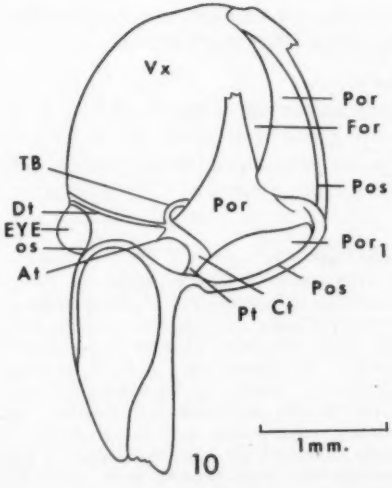
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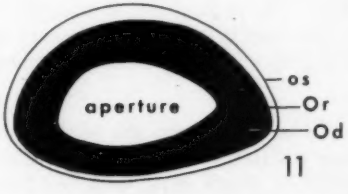
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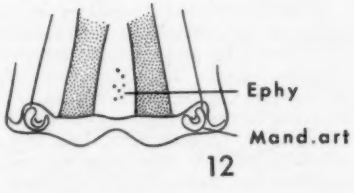
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A pair of discontinuous sutures (Fig. 8, f) arise immediately below the eyes and extend distally to the hypostomal area (Hst), terminating at the maxillary articulation (Max. art). These sutures are probably the same as those found in *Pissodes strobi* (Peck) and described by Hopkins (1911) as, "the divergent arms of a single gular suture". However, a close examination of *H. warreni* and *P. strobi* reveals that these sutures do not diverge from the so-called "gular suture" (Pos_1). These sutures (f) are apparently secondary and therefore probably lack morphological significance but it is possible that they are remnants of the subgenal suture of Snodgrass (1935) that have become distorted by the pronounced elongation of the postgenal area of the head.

There are three small sclerites situated in the ventral area of the occipital foramen (Fig. 8, c, d, e). These sclerites are fused with the margin of the head capsule and serve as areas of muscle attachment. According to Henry (1958), they represent remnants of the cervical sclerites that have fused with the head capsule, and have been found in all species of Coleoptera studied by her.

The compound eyes are ovoid in shape with hexagonal facets. The ocular suture (Fig. 11, os) is most prominent on the outside edge of the eye and is inflected to form a strong ocular ridge (Or). The ocular ridge forms a base upon which the ommatidia of the eye rests. The eye in this species also contains a large ocular diaphragm (Od) which, according to Ferris (1940), is not present in all insects.

Head Appendages

Antennae

The antennae (Fig. 17) are clavate and geniculate, arising near the mouth and lying in the long antennal grooves (Fig. 9, Atg). The antennal socket (Ats) forms the base of the antennal groove (Atg) which extends nearly to the eye. The antennal scrobe (Hopkins, 1911) and the antennal bulb (Comstock, 1948) form the base of the scape (Fig. 17, As, Ab, S), and articulate with the antennifer (Fig. 9, An) which is located on the mesodorsal edge of the antennal socket. The scape (Fig. 17, S) is sparsely setaceous and is nearly as long as the funicle (F). The pedicel (P) is more than twice the length of any but the first segment of the funicle. Both the pedicel and the funicle are clothed with long bristles. The club (CL) is globose, 4-segmented, and bears a few short bristles.

Mouthparts

The mouthparts are of the chewing type and occur at the distal end of the long rostrum. The mandibles are large, strong and well suited for tearing off pieces of tough bark, both for food and in the preparation of oviposition sites. The clypeus and labrum are not differentiated from the frons. The epipharynx

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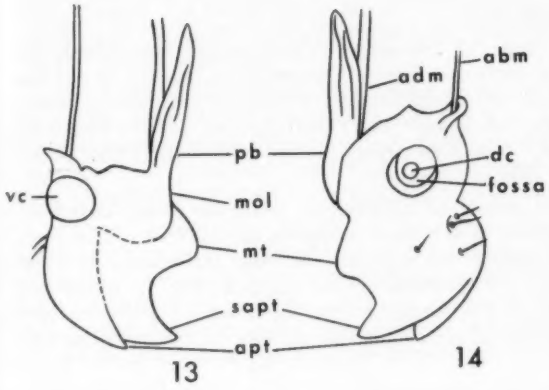
All figures refer to *H. warreni* unless otherwise indicated.

Figs. 13-20, head appendages and thorax. 13, inside aspect of right mandible; 14, outside aspect of right mandible; 15, hypopharynx; 16, maxilla; 17, antenna; 18, antennal scape of *H. pinicola;* 19, prothorax; 20, mesonotum. Ab, antennal bulb; abm, abductor muscle; adm, adductor muscle; apt, apical tooth; As, antennal scrobe; Bp, basal plate of hypopharynx; Bs, basisternum; Cd, cardo; CL, club; dc, dorsal condyle; Eu, eusternum; F, funicle; g, bridge of hypopharynx; Ga, galea; Gat, galeal tooth; h, prothoracic bristles; La, lacinia; LbPlp, labial palpus; Lct, lacinial teeth; Lin, lingua; Mand. art., ventral mandibular articulation; mc, maxillary condyle; Mlp, maxillary palpus; mn, median notal suture; mol, molar surface of mandible; mt, median tooth; NP, notal wing process; P, pedicel; pb, pharyngeal bracon; Pge, postgena; ph, pleural hook; Plpfr, palpifer; Pra, prealar arm; Prsc, prescutum; S, scape; SA, sternal apophysis; sa, pit of sternal apophysis; sapt, sub-apical tooth; Scl, scutellum; scs, sternacostal suture; Sct, scutum; Sga, subgalea; Sl, sternellum; spn, spinasternum; Stp, stipes; vc, ventral condyle; vs, scuto-scutellar suture.



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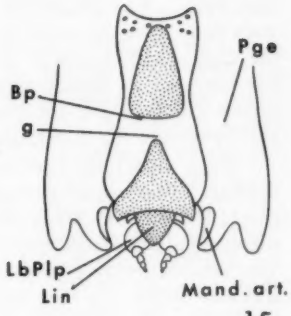

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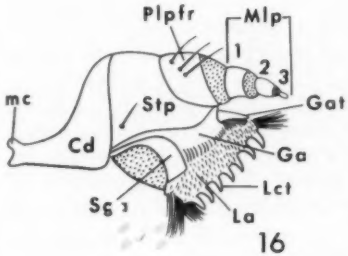

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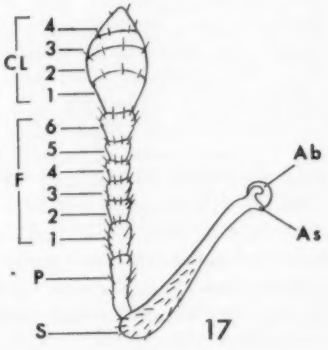

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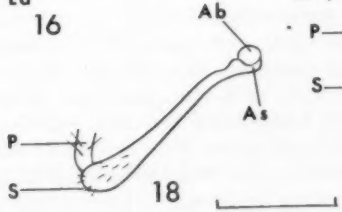

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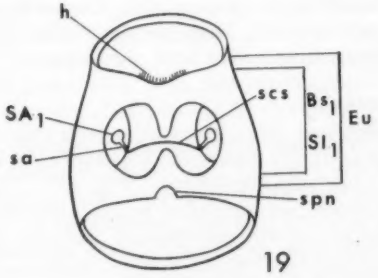

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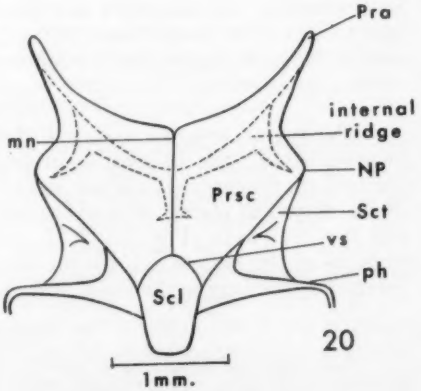

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(Fig. 12, Ephy) is a membranous structure that is continuous with the internal fold of the epistomal area of the head.

Mandibles.—The mandibles (Figs. 13, 14) are stout and heavily sclerotized, each with four setae on its dorsal surface. The left mandible is slightly larger than the right, overlapping it at the tip when closed. The inner mandibular margin has three teeth, apical (apt), sub-apical (sapt) and median (mt). The molar region (mol) is not toothed. The pharyngeal bracon (Hopkins, 1909) is long and covered with fine setae (Fig. 13, pb).

Each mandible has two points of articulation with the head, dorsal and ventral. The dorsal articulation is the more complex of the two. The dorsal condyle (Fig. 14, dc) is surrounded by a prominent fossa and rotates in a fossa surrounded by a large ridge on the epistomal area of the face (Fig. 12, Mand. art). The ventral condyle (Fig. 13, vc) is located on the inner aspect of the mandible and articulates in a crescent-shaped acetabulum in the base of the postgena (Fig. 15, Mand. art).

Maxillae.—The maxillae (Fig. 16) appear to contain all the components found in the generalized insect. The cardo (Cd) articulates with the rostrum (Fig. 8, Max. art) by a basal condyle (mc). The cardo (Cd), stipes (Stp) and palpifer (Plpfr) are separated by distinct sutures. The three-segmented palpus (Mlp) is distal to the palpifer. All these components bear numerous bristles and contain sensory pores. The galea (Ga) and the lacinia (La) form a single large lobe arising from the stipes (Stp). The mesal side of the lobe, "lobus internus" of Schedl (1931), bears a row of lacinial teeth (Lct) and many bristles of varying length. The outer side of the lobe "lobus externus" is more heavily sclerotized, terminating in a strongly sclerotized galeal tooth (Gat). The basal portion of the outer lobe or galea (Ga) bears a sclerotized bar which fuses with the base of the stipes and represents the subgalea (Sga).

Labium and Hypopharynx.—The only areas of the labium associated with the feeding mechanism in this insect are the mentum (Fig. 8, Mt) and the distal prementum (Prmt) with its pair of 3-segmented labial palpi (Lbplp). The prementum acts as a lower lip, being freely movable and hinged to the mentum at the labial suture (lbs). It lacks ligular differentiation found in some Rhynchophora (Schedl, 1931) unless the small distal projection (Lig) may be assumed to represent the remnant of such a structure. The mentum supports the maxillary articulations and is fused with the hypopharynx.

The hypopharynx (Fig. 15) is a large membranous area forming the preoral food chamber. It contains a heavily sclerotized basal plate (Bp) resembling a figure "H". The bar of the "H" is fused with the mentum (g). The distal area of the hypopharynx bears a membranous tongue-like lobe, the lingua (Lin).

Thorax

The thorax (Fig. 6) is clearly divided into three parts, of which the first or prothorax is quite different in structure from the meso- and metathorax. The last two are similar and together present a unit, the pterothorax (Fig. 25). Most of the tergal and pleural areas of the pterothorax are concealed beneath the elytra and the prothorax (Fig. 1). The scutellum of the mesothorax and the episternum of the metathorax are the only elements that are clearly visible. The prothorax is as long as the meso- and metathorax combined.

Prothorax

This segment (Fig. 19) is heavily sclerotized, deeply punctate and sparsely clothed with hairs. It is longer than wide and constricted at each end. The

tergal, pleural and sternal areas are fused, forming a continuous tube, with infolded ends. A small "brush" of fine hairs (Fig. 19, h) occurs on the ventrocephalic end of this tube.

The entire dorsal aspect is occupied by the pronotum, which is widest at the middle and nearly conceals the head (Fig. 2). The median carina (Ca) and its corresponding weak depressions are useful taxonomic characters. The lateral margins of the pronotum bend sharply downward to form continuous lateral plates. Definition of the pleural elements is obscured by the absence of sutures.

The eusternum (Fig. 19, Eu) of Snodgrass (1935) is fused with the spinasternum, which may be recognized by the presence of a weak spina (spn). The eusternum is subdivided, by a sternacostal suture (scs), into a basisternum (Bs_1) and a sternellum (Sl_1). The apodemal apophyses (SA_1) of the eusternum are typical, originating as invaginations of the integument. Weak pits (sa) mark their point of origin which is at the lateral ends of the sternacostal suture (scs).

Pterothorax

The pterothorax is not functional as a region of wing motivation in the vestigial-winged *H. warreni.* However, most of the elements common to this region in functional pterygote insects, can be recognized. Although more weakly developed, the pterothorax resembles that of the closely related winged species, *H. pinicola.* This resemblance is utilized to strengthen certain morphological theories advanced in this section of the paper.

As in all Coleoptera, the mesothorax is greatly modified and reduced. For this reason, the areas of the more generalized metathorax are described before attempting to define their respective counterparts in the mesothorax.

Metanotum.—The major tergal elements, prescutum, scutum, scutellum, and postnotum, are represented in the metanotum (Fig. 21). The antecostal suture (acs) terminates cephalically in the intersegmental membrane (ism). This indicates the absence of a precosta which, according to Snodgrass (1935), lies anterior to the antecostal suture. The integument is inflected ventrally at the antecostal suture to form a small median antecosta (Ac). The phragma is rudimentary and cannot be differentiated from the antecosta.

Snodgrass (1927) interprets the boundaries of the insect prescutum (Prsc) as an anterior antecostal suture (acs) and a posterior transverse or prescutal suture (ts), with the lateral edges of the intervening sclerite (Prsc) being produced to form the prealar arms (Pra). He also states, "In the metathorax of Coleoptera the prescutum (Prsc) reaches its highest development, its median part being here often expanded posteriorly until it almost meets the apex of the scutellum (Scl)." In this insect much of the prescutum is reduced to a membranous area (mb) called the "anterior membrane" by Schedl (1931).

Perhaps the most notable modification of the metanotum of Coleoptera is the so-called "alacristae" of Crampton (1918) or the "scutellar groove" of Hopkins (1909). It is a structure adapted to accommodate the elytra when they are at rest. The scutellar groove (Fig. 21) and the exceptional development of the prescutum divide the scutum (Sct) into two lateral lobes. This is an abnormal modification. By definition, the scuto-scutellar suture (vs) divides the alinotum into an anterior scutum and a posterior scutellum (Snodgrass, 1935). In *H. warreni* the scuto-scutellar suture (vs) is weak and becomes lost in the scutellar groove. The V-shaped ridge, that normally marks the suture internally, is absent in this species but is prominent in *H. pinicola* (Fig. 22, VR). By following this ridge in the latter species it is possible to trace the scuto-scutellar suture (vs) and

find that it advances cephalad to the anterior membrane (mb) of the prescutum (Prsc). This indicates that the scutellar groove belongs to the scutellum (Scl) and modifies it so that it divides the scutum (Sct) into two lateral halves as well as dividing the alinotum anteriorly and posteriorly in the usual manner described by Snodgrass.

Although greatly modified, the scutum (Fig. 21, Sct) still occupies most of the surface area of the alinotum. Each lateral area bears an anterior notal wing process (ANP) and a posterior notal wing process (PNP). Sclerotization is light and sutures are weak. There are two pairs of rudimentary sutures, called intra-scutellar sutures by the author. One pair (iss_1) arises near the cephalic end of the scutellar groove and the other (iss_2) at the base of the anterior notal wing process (ANP). The same sutures in *H. pinicola* are more strongly developed, (Fig. 22) and the area of the scutum enclosed by them is raised to form a distinctive, heavily sclerotized plate.

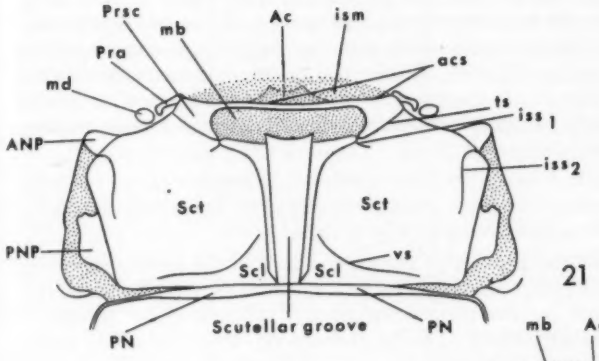
The postnotal plate of the metanotum (Fig. 21, PN) is a weak, poorly defined structure without a phragma. According to Jackson (1928) weakness of postnotal plates and absence of phragmata occur in flightless Coleoptera. The postnotal plate of *H. pinicola* (Fig. 22, PN) is a well defined structure but lacks a phragma.

Mesonotum.—The mesonotum (Fig. 20) is a complex structure and it is virtually impossible to define its elements without reference to the more generalized metanotum (Fig. 21). In describing the genus *Gnathotrichus*, Schedl (1931) says, "the largest area of the mesonotum is occupied by the triangular prescutum". This statement may be accepted only if one follows the basic principles as they were applied in defining the elements of the metanotum. These indicate that the prealar arms (Pra) are ventro-lateral extensions of the prescutum (Prsc); the scuto-scutellar suture (vs) separates the prescutum from the scutellum (Scl) and divides the scutum (Sct) into two lateral lobes; the scutum (Sct) bears the notal wing processes (ANP, PNP). Figure 20 indicates the way in which these principles were applied to name the elements of the mesonotum. However, certain modifications in these elements require further description.

The prescutum (Fig. 20, Prsc) is bisected by a median notal suture (mn) and has a very large internal ridge. This ridge, or bridge, is common to the mesonotum throughout the order. At first, it appears that the notal wing processes are part of the prescutum. Close examination shows that this is not the case but that the scutum is ventral to the prescutum at this point and that the wing articulates at one point only, on the scutum (NP).

All figures refer to *H. warreni* unless otherwise indicated.

Figs. 21-27, thorax and abdomen. 21, metanotum; 22, metanotum, *H. pinicola;* 23, external aspect of meso- and metasterna; 24, internal aspect of meso- and metasterna; 25, lateral aspect of meso- and metathorax; 26, abdominal $sternites_{3-7}$; 27, abdominal $sternites_{3-4}$ of *H. pinicola.* Ac, antecosta; acs, antecostal suture; ANP, anterior notal wing process; Ba, basalare; Bs, basisternum; Cx, coxa; Cx_s. art., articulation of sternellum and coxa; cxs, coxal suture; Epm, epimeron; epm, postepimeron; Epm_2. art., eps_3. art., metasternal articulations; Eps, anepisternum; eps, katepisternum; es, episternal suture; Fu, furca; Hp, abdominal hypopleurite; icp, intercoxal process; ism, intersegmental membrane; iss, intra-scutellar suture; mb, anterior membrane; md, muscle disc; Meso-n, mesonotum; Meta-n, metanotum; pepmh, postepimeral hook; pepmh. art., abdominal thoracic articulation; Peps, preepisternum; PLA, pleural apophysis; PLS, pleural suture; PN, postnotal plate; PNP, posterior notal wing process; Pra, prealar arm; Prsc, prescutum; sa, pit of sternal apophysis; Se, subalare; SA, sternal apophysis; Scl, scutellum; scs, sternacostal suture; Sct, scutum; sh, sternal hook; sh. art., articulation of sternum; Sl, sternellum; Sp, spiracles (1, 2, thoracic); St, thoracic sternum; St. art., articulation of abdominal sternite; Stn, abdominal sternite; T, abdominal tergite; ts, transverse suture; VR, v-shaped ridge; vs, scuto-scutellar suture; Wp, wing process.



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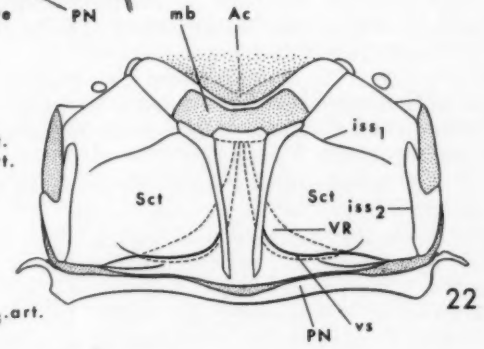

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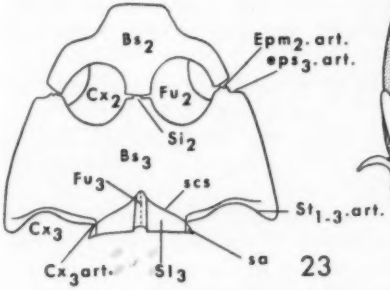

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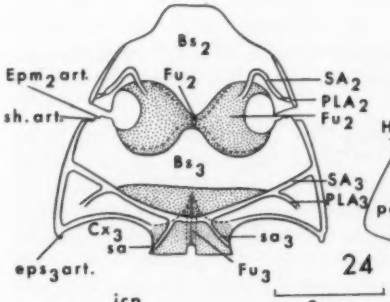

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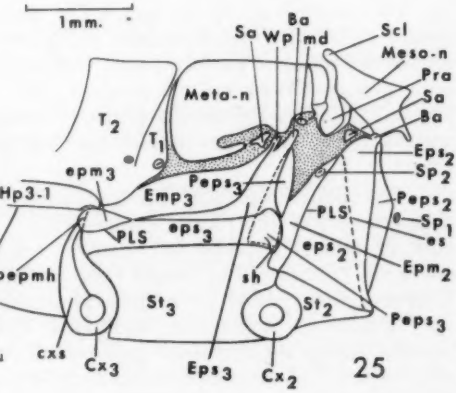

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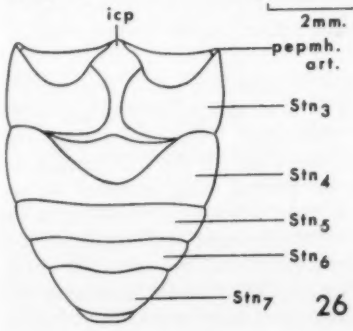

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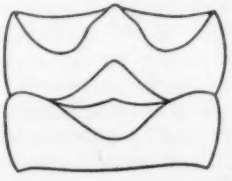

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The scutum (Sct) is smaller than the prescutum (Prsc) and appears to be divided into two lobes by the scutellum (Scl). However, its caudal edge is fused to the ventral aspect of the scutellum and is extended laterally to form a pair of arms, "pleural hooks" (ph) of Schedl. These arms might easily be mistaken for a postnotal plate, especially in newly emerged adults, when they may be readily separated from the scutum. A postnotal plate does not occur in the mesonotum of Coleoptera (Snodgrass, 1935).

The scutellum (Scl) is a small, heavily sclerotized, triangular plate. It is the only portion of the mesonotum that is exposed dorsally, the remainder being covered by the pronotum and the elytra (Fig. 2, Scl).

Metapleuron.—The sclerotized portion of the pleural area of the metathorax (Fig. 25) is occupied by two large primary plates, the episternum and the epimeron. These plates are separated by the pleural suture and subdivided by secondary sutures. The pleural suture (PLS) appears continuous with the coxal suture (cxs) and extends from the coxal cavity (Cx_3) of the leg to the articular process of the wing (Wp). This suture is represented internally by a prominent ridge, the pleural apophysis. According to Snodgrass (1935), the pleural suture usually follows a direct course. However, in *H. warreni,* as in many highly specialized insects, its course is irregular.

The episternum is divided into two parts by a secondary suture called the episternal suture (es) by Kaston (1936). The ventral part is known, by most authors, as the "katepisternum" (eps_3). This is the only portion of the pleuron that is exposed below the elytra in Coleoptera and is referred to by systematists as the "episternum". It is a long, heavily sclerotized, deeply pitted plate, terminating in a ventro-cephalic hook. This hook is called the "sternal hook" (sh) by Schedl (1931). It fits into an emargination of the sternum that he calls the "clavicula" (Fig. 24, sh. art). The dorsal portion of the episternum is commonly called the "anepisternum" (Fig. 25, Eps_3). It is smooth, less heavily sclerotized than the katepisternum, and is produced dorsally to form the articular wing process (Wp) and the basalare (Ba). As indicated by the dotted line in Figure 25, the pre-episternum ($Peps_3$) is a large structure. It is lightly sclerotized and much of it is hidden beneath the anepisternum (Eps_3) and the katepisternum (eps_3).

The epimeron proper (Epm_3) is a flexible, partly membranous sclerite, lying dorso-caudad to the pleural suture (PLS). A secondary branch of this suture cuts off a small, heavily sclerotized piece of the epimeron to form the postepimeron (epm_3). The caudal edge of the postepimeron is inflected to form a recurved hook (pepmh), the "postepimeral hook" of Schedl, that articulates with the "clavicula" of the first abdominal sternum (Fig. 26, pepmh. art). The cephalic end of the combined hypopleurites of the first three abdominal segments (Fig. 6, Hp3-1) articulates with a shallow emargination on the dorsal edge of the postepimeron (Fig. 25, epm_3).

The epipleurites include the basalare (Ba) and the subalare (Sa). According to Snodgrass (1935) they "appear to be derived by a secondary separation from the upper edges of the episternum and the epimeron". He also states "the basalare is frequently but an imperfectly separated lobe of the episternum or merely an area on the latter to which the anterior pleural wing muscles are attached". Hopkins (1909), Schedl (1931) and Kaston (1936), all working with Rhynchophora, place a different interpretation on the location and names of the epipleurites. These authors consider the basalare (Ba) and the articular wing process (Wp) as the anterior and posterior wing processes which they call the "clavicle" and "coracoid" respectively. The sclerite that Kaston calls the basalare

appears to be a preepisternum. Hopkins and Schedl call it a "clavicle disc" or "pronator disc". These interpretations do not satisfy the requirements established for epipleurites by Snodgrass nor do they appear to fit the anatomical structures as they occur in *H. warreni*. In this insect the basalare (Ba) is an imperfectly separated lobe of the episternum that serves as a point of attachment for the anterior pleural wing muscles. Furthermore, the preepisternum ($Peps_3$) appears to originate on the ventral edge of the katepisternum (eps_3) as a well defined sclerite of some proportions and therefore cannot be considered as either a basalare or a muscle disc as suggested by the above group of authors. A small muscle disc (md) occurs between the basalare (Ba) and the prealar arm (Pra). It appears to be connected to the prealar arm by a ligament but intensive investigation would be necessary to determine its purpose and to homologize it with similar elements in other groups.

The subalare (Sa) of the metapleuron is an independent sclerite located in the membranous area at the base of the wing caudad to the articular wing process (Wp). It is triangular in shape and is heavily sclerotized.

Mesopleuron.—The largest sclerite of the mesopleuron is the episternum (Fig. 25, Eps_2, eps_2). It is heavily sclerotized and roughly pitted, triangular in shape, with the broad base of the triangle bordering the sternum (St_2). It is divided into a basal katepisternum (eps_2) and a dorsal anepisternum (Eps_2) by an internal ridge that is marked externally by a weak trough which is concealed by the overlapping prothorax (Fig. 6, Pro-n). This trough represents the secondary episternal suture (Fig. 25, es). The anepisternum (Eps_2) terminates dorsally in a broad articular wing process (Wp) and a prominent, imperfectly separated, dorsocephalic lobe, the basalare (Ba). The preepisternum ($Peps_2$) is a smooth, lightly sclerotized, triangular sclerite extending along the cephalic edge of the anepisternum (Eps_2).

The epimeron (Epm_2) is a long, narrow, flexible, partly membranous sclerite, separated from the episternum by the pleural suture (PLS). The epimeron is not subdivided into secondary areas.

The subalare (Sa) of the mesopleuron is a small rounded sclerite situated in the membranous tissue at the base of the wing, caudad to the wing process (Wp).

The two pairs of thoracic spiracles appear to belong to the mesopleuron. The first (Sp_1) is located in the intersegmental membrane preceding the preepisternum ($Peps_2$). The second spiracle (Sp_2) is concealed by the dorsal edge of the epimeron (Epm_2). According to Snodgrass (1935), embryonic evidence indicates that thoracic spiracles belong to the meso- and metathoracic segments and other positions assumed by them in adult insects are secondary. Therefore, Sp_1 represents the mesothoracic spiracle and Sp_2, the metathoracic spiracle.

Pterothoracic Sterna.—Externally the meso- and metasterna (Fig. 23) appear as two separate but closely associated, heavily sclerotized plates. The plates are sparsely clothed with yellowish-white setae that are produced from individual pits in the integument. The two segments are united internally by the furca (Fig. 24, Fu_2) which is an elaborate development of the sternellum (Fig. 23, Sl_2) or furca-sternum of the mesothorax.

The furca (Fu_2) is a strong inflection of the sternellum (Fig. 23, Sl_2). It differs from the generalized type in that it is projected laterally into partly membranous tissue that covers nearly all the coxal cavities. The sternal apophyses (Fig. 24, SA_2) are supported by this membranous tissue. They are projected toward the prothorax and recurve to unite with the pleural apophyses (PLA_2). The mesothoracic sternal apophyses differ from the generalized type in that

they do not appear to have external pits at their bases but rather they seem to be inflections of the semi-membranous extensions of the furca. Also, there is no evidence of a sternacostal suture between their bases. Because of these modifications the eusternum is not divided into a definitive basisternum and sternellum. However, if one accepts the theory advanced by Snodgrass that the sternellum gives rise to the furca, the area between the coxae of this insect may be designated as the sternellum (Sl_2) of the mesothorax and the area cephalad to the coxae as the basisternum (Bs_2). The basisternum (Bs_2) forms the largest part of the mesosternum. It is a simple plate without secondary sutures or special structures for articulation with other elements.

The basisternum of the metathorax (Fig. 23, Bs_3) is more than twice as large as that of the mesothorax. It is deeply inflected along its outer edges for the articulation of other elements. The cephalo-lateral edges each bear two notches (Fig. 24, Epm_2. art. sh.art), the inner one for articulation with the mesothoracic epimeron (Fig. 25, Epm_2), and the outer one for articulation with the sternal hook (sh) of the metathoracic katepisternum (eps_3). The caudo-lateral corners (Fig. 24, eps_3. art) have an internal concavity for articulation with the caudo-ventral edge of the metathoracic katepisternum (Fig. 25, eps_3). The basisternum (Fig. 23, Bs_3) is divided from the sternellum (Sl_3) by the sternacostal suture (scs) which arises at the pits (sa) of the sternal apophyses (Fig. 24, SA_3).

The sternellum (Fig. 23, Sl_3) may be examined only after removal of the abdomen. It is a triangular structure with a mesal inflection that accommodates the intercoxal process of the abdomen (Fig. 26, icp). The caudo-lateral edges of the sternellum are curved to form an acetabulum for articulation with the coxae (Fig. 23, Cx_3. art). The furca (Fig. 24, Fu_3) is marked externally as a median groove. The sternal apophyses (SA_3) arise as invaginations of the integument within the acetabulum formed for articulation with the coxae (Fig. 23, Cx_3. art). The apophyses (Fig. 24, SA_3) are greatly enlarged and diverge to form an arch that extends to the lateral edges of the basisternum. There is a large area of membranous tissue between much of the arch as shown in Fig. 24. The pleural apophyses are connected with the sternal apophyses by ligamentous strands indicated as PLA_3.

Thoracic Appendages

Legs.—The three pairs of legs possess the following segments: coxa, trochanter, femur, tibia, tarsus, and pretarsus. The legs are long and slender but each pair differs from the other in some characteristics. For the sake of simplicity the elements of the prothoracic or fore-leg will be described in detail, followed by a discussion of variations that occur in the three pairs of legs.

The coxa (Fig. 28, Cx_1) is nearly spherical and has a prominent basicoxite (Bcx) with a distinguishing basicostal suture (bcs) and its internal ridge, the

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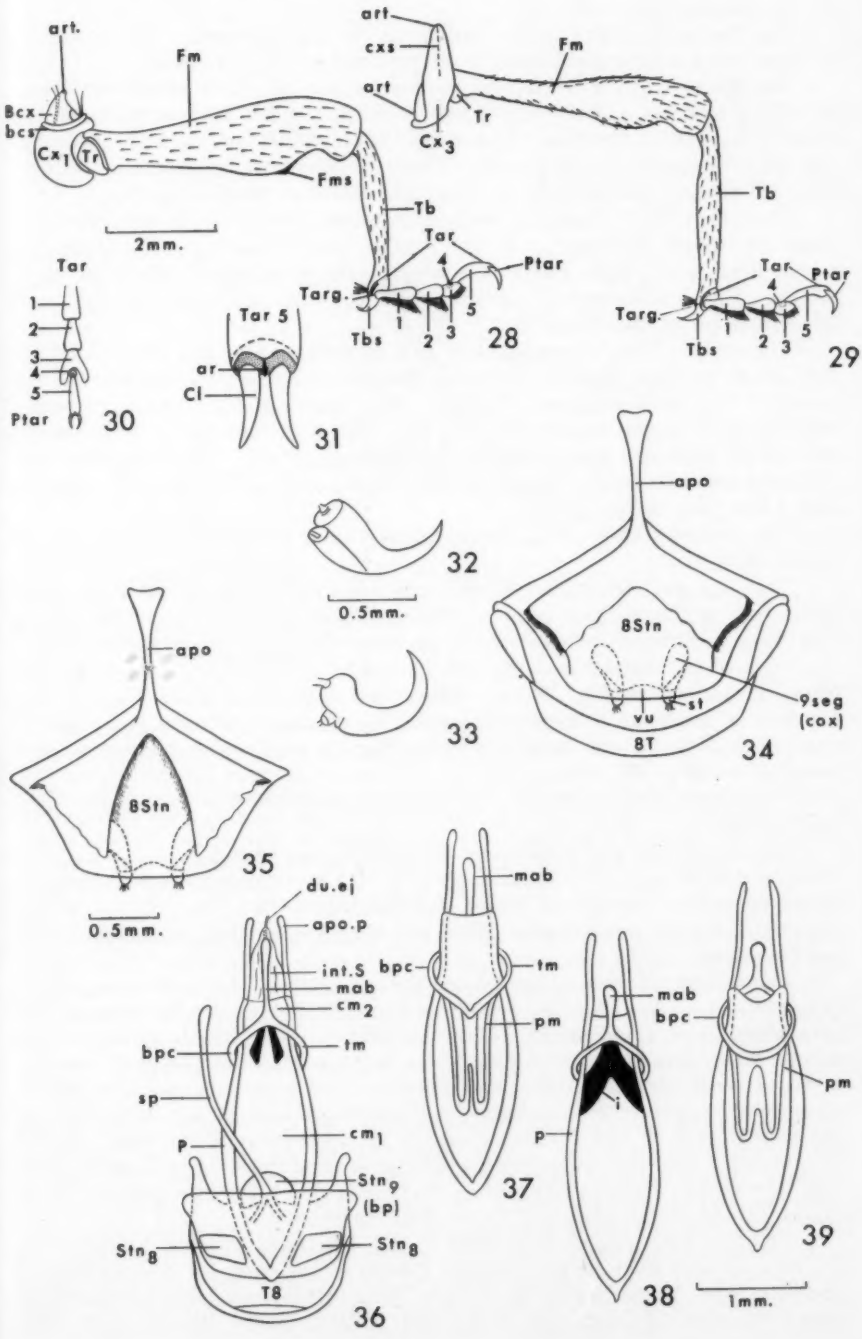
All figures refer to *H. warreni* unless otherwise indicated.

Figs. 28-39, thoracic and abdominal appendages. 28, outside aspect of fore leg; 29, inside aspect of hind leg; 30, tarsus; 31, pretarsus; 32, 33, spermatheca (33 *H. pinicola*); 34, 35, female genital segments (35, *H. pinicola*); 36, 37, ventral and dorsal aspects of penis valve; 38, 39, ventral and dorsal aspects of penis valve *H. pinicola*. apo.p., apophysis of penis; ar, arolium; art., point of articulation; bcs, basicostal suture; Bcx, basicoxite; bpc, basal piece of tegmen; Cl, claws; cm_1, cm_2, connecting membranes; Cx, coxa; cxs, coxal suture; du. ej., ejaculatory duct; Fm, femur; Fms, femoral spur; i, pigmented area of internal sac; int. s., internal sac; mab, manubrium; p, penis; pm, paramere; Ptar, pretarsus; sp, spicule; Stn (bp), basal piece of 9th sternite; Stn, 8th abdominal sternite; T, abdominal tergite; Tar, tarsus; Targ., tarsal groove; Tb, tibia; Tbs, tibial spur; tm, tegmen; Tr, trochanter.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p
38
39
1mm.

basicosta. The basicoxite (Bcx) forms a single point of articulation between the leg and the body wall.

The trochanter (Tr) is the smallest of the leg segments. It is triangular in shape and is immovably joined to the proximal end of the femur.

The femur (Fm) is the largest segment of the leg. It is somewhat clavate in outline and has a deep groove at its distal end for the reception of the articular condyle of the tibia. It may also have a small spur on its ventral edge near the proximal end of the groove. The size of the spur varies with individuals. It is well defined in some (Fig. 28, Fms) and absent in others (Fig. 29).

The tibia (Tb) is a slender, straight segment, not as stout as the femur and about two-thirds its length. It has a pronounced tarsal groove (Targ.), a strong tibial spur (Tbs), and a few stout bristles at its distal end. The tarsal groove (Targ.) is located on the outside of the tibia and represents the point of articulation of the tarsus.

The tarsus (Tar) is composed of five segments. The first and second are cylindrical in shape, slightly expanded distally, with the first longer than the second. The third segment is bilobed. The fourth is very small and visible only from the dorsal aspect (Fig. 30, 4). The fifth segment is long, slender and curved ventrally, terminating in the pretarsus (Ptar). Tarsal segments one to three have pads of short bristles on their ventral surfaces and all tarsal segments bear a few long dorsal bristles.

The pretarsus (Fig. 31) is composed of a small arolium (ar) and a pair of simple claws (Cl).

The pro- and mesocoxae are similar in shape and structure but differ from each other in the position of the fossa for the articulation of the trochanter. The fossa is directed caudad in the procoxa and cephalad in the mesocoxa. The coxa of the metathoracic leg differs markedly from that of the other two pairs. It is elongate (Fig. 29, Cx_3) rather than spherical (Fig. 28, Cx_1); it does not have a basicoxite or basicostal suture; it articulates with the body wall at two points (Fig. 29, art) rather than one (Fig. 28, art); and it has a prominent coxal suture (Fig. 29, cxs).

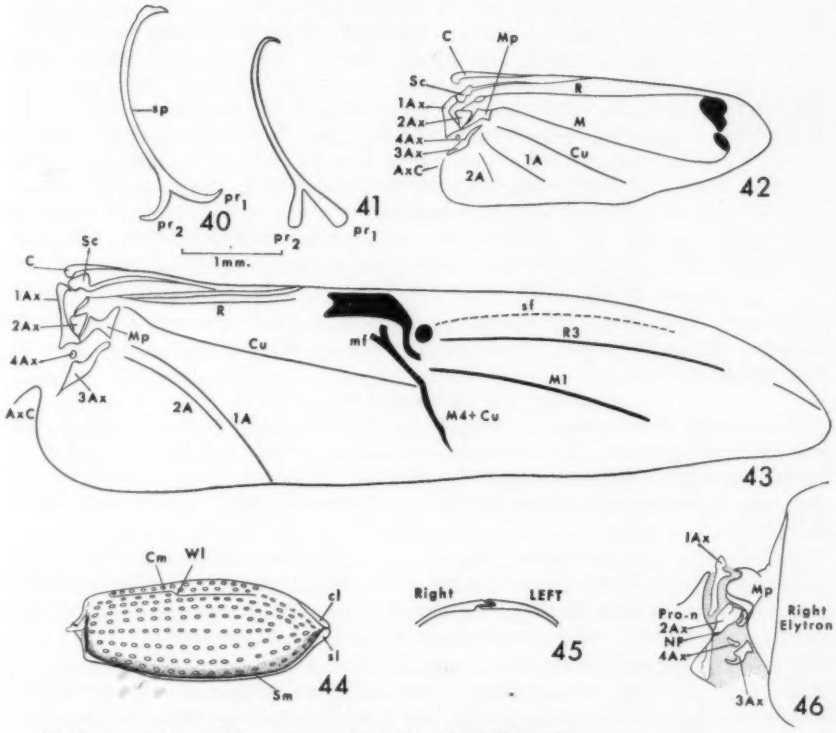
The femur of the fore leg is stouter and straighter than it is in the other pairs of legs.

The tibiae, tarsi and pretarsi are alike in all pairs of legs.

Metathoracic Wings.—The hind wings (Fig. 42) are membranous and vestigial, extending only to the second visible abdominal sternum. The veins are poorly developed and do not branch. They are named according to Forbes (1922) and Snodgrass (1935).

The axillary sclerites or pteralia are well developed. Axillaries one to three (Fig. 42, $1A_x$, $2A_x$, $3A_x$) are heavily sclerotized and similar in shape to the generalized type described by Comstock (1918). The fourth axillary ($4A_x$) usually assumed to be absent in Coleoptera, is present but vestigial in *H. warreni*. It lies between the third axillary and posterior notal wing process. The median plate (Mp) is a poorly defined, lightly pigmented membranous area, lying between the second axillary ($2A_x$) and the origins of the medio-cubital veins. Schedl (1931) called a sclerite occupying the same position in the wing of *Gnathotrichus* spp., the fourth axillary. According to Comstock (1918) this position is occupied by the median plate, not by the fourth axillary.

The first wing vein or costa (Fig. 42, C) articulates with the basalare (Fig. 25, Ba). It continues along the costal margin of the wing for a short distance and fuses with the subcosta (Fig. 42, Sc). The subcosta (Sc) has a twisted head that articulates with the head of the first axillary sclerite (1Ax). The radius



All figures refer to *H. warreni* unless otherwise indicated.

Figs. 40-46, thoracic and abdominal appendages. 40, 41, male genital spicule (41, *H. pinicola*); 42, 43, hind wing (43, *H. pinicola*); 44, inside aspect of left elytron; 45, wing lock of sutural margin; 46, pteralia of fore wing. 1A, 2A, anal veins; 1Ax-4Ax, axillary sclerites; AxC, axillary cord; C, costal vein; cl, costal lobe; Cm, costal margin; Cu, cubital vein; M, medial vein; mf, median fold; Mp, median plate; NP, notal wing process; pr, fork of spicule; R, radial vein; Sc, subcostal vein; sf, scutellar fold; sl, sutural lobe; Sm, sutural margin; sp, spicule; Wl, wing lock.

(R) arises from the second axillary (2Ax) as a thin inconspicuous vein. It continues nearly to the apical margin of the wing and terminates in a pigmented area. The medial vein (M) originates at the median plate (Mp) and like the radius, continues nearly to the apical margin of the wing and terminates in a second pigmented area. The cubital vein (Cu) is short, and arises near the median plate (Mp). There are two inconspicuous anal veins (1A, 2A) arising near the third axillary sclerite.

Mesothoracic Wings.—The form and general appearance of the elytra can be seen from Figs. 1, 2 and 4. The sutural margin (Fig. 2, Sm) is straight but the costal margin (Fig. 4, Cm) is curved dorsally over the meso- and metathorax, exposing the episternum (Fig. 1). The elytra are very heavily sclerotized, thick and tough and contain no wing veins. Each has ten longitudinal rows of punctures. The interspaces are raised and bear scattered clumps of short yellowish-white setae. Both elytra are fitted with grooved ledges along their sutural margins (Fig. 44, Sm). These ledges form a locking system, with the right elytron fitting into the left (Fig. 45). The ledges terminate apically in flattened lobes (Fig. 44, sl), the

left over the right. The facing surface of each lobe is roughened by the presence of very fine striae. Various authors (Hopkins, Schedl, Kaston) have defined similar lobes in bark beetles as stridulating organs. The inner side of the costal margin is also fitted with a longitudinal groove (Fig. 44, Cm). This groove is deepened at the point where each elytron contacts the anterior margin of the hypopleura of the first visible abdominal segment (Fig. 6, Hyp. 3-1). Schedl (1931) called this structure the lateral wing lock (Fig. 44, Wl). The groove of the wing locks over the anterior edge of the hypopleura to keep the elytra closed when at rest. The costal margin terminates in a concave flattened area on the inner apical surface (cl), similar to the lobe of the sutural margin. However, the costal lobe (cl) has much finer striae than those of the sutural lobe (sl).

The pteralia of the mesothorax (Fig. 46) are very similar to those of the metathorax (Fig. 42). By using the latter as a guide one can orientate the elements of the mesothorax. All components (1Ax, 2Ax, 3Ax, 4Ax, Mp) are represented.

Abdomen

The abdomen is heavily sclerotized ventrally, and sparsely clothed with yellowish-white setae. Dorsally it is completely covered by the elytra (Fig. 1). There are eight abdominal segments although only seven tergites are normally apparent in the female, the eighth being withdrawn beneath the seventh (Figs. 6, 7).

Tergites.—The first six tergites (Fig. 6) are lightly sclerotized and separated by wide membranous areas. The seventh and eighth tergites are heavily sclerotized and covered with setae distally. Elements of the primitive ninth and tenth segments are modified to form components of the genital structures.

Pleurites.—The area between the tergites and sternites is commonly differentiated into epipleurites and hypopleurites. According to Snodgrass (1935), "there is no morphological justification for the use of this terminology since nothing above the dorso-pleural line or below the pleuro-ventral line belongs to the pleural region". There are no differentiating lines or folds in the pleural area of the adult of this insect. However, the spiracles (Fig. 6, Sp) are considered as occurring in the membranous epipleural area. The "hypopleurites" (Hp) are assumed to be the heavily sclerotized smooth plates ventral to this membranous area and fused with the sternites (Stn). Snodgrass prefers to use the term "laterosternite" or "pleurosternite" because these plates represent the region of the primitive limb bases. Each definitive sternite, including the eighth, that is normally concealed within the seventh, bears a characteristic hypopleurite (Fig. 6, Hp). The first three hypopleurites are fused to form a single elongate sclerite (Fig. 6, Hp 3-1).

Sternites.—Only five abdominal sternites, the third to the seventh, inclusive, are defined by distinctive sutures. Sternite three (Fig. 26, Stn_3) is produced into a large intercoxal process (icp). Numbers one and two form the coxal cavity and are represented by two indistinct sutures in *Dendroctonus* (Hopkins, 1909). These sutures are not apparent in *H. warreni.*

All of the visible sternites are heavily sclerotized, deeply pitted, and clothed with yellowish-white setae. The first (Stn_3) has a deep median depression which extends shallowly into that of the second (Stn_4). These two sternites are fused but the remainder are flexible at the intersegmental line, the seventh being the most flexible. The eighth sternite is retracted beneath the seventh and is described with the genitalia.

Abdominal Spiracles.—There are eight pairs of abdominal spiracles in the female and seven in the male of this species (Fig. 6, I-VIII Sp.). The first six are located in the membranous epipleural area. Spiracles seven and eight in the female, and

seven in the male, are located at the bases of the corresponding tergites. Spiracle one (I Sp) is much larger than the others. Spiracles two to seven are about one-half the size of one but well developed. Spiracle eight (VIII Sp) occurs only in the female and is rudimentary.

Hopkins (1911) reported seven pairs of abdominal spiracles in both sexes of *Pissodes* and eight for *Dendroctonus* but he considered the eighth rudimentary (1909). Schedl (1931) reported eight pairs of spiracles in the male and seven in the female of the genus *Gnathotrichus* but he states, "the eighth pair of spiracles in the male are always rudimentary". The above observations indicate that there is considerable variability in the number of spiracles between sexes and between taxonomic groups of Rhynchophora. It appears, however, that all individuals have seven pairs of functional abdominal spiracles.

Abdominal Appendages

The abdominal appendages are composed of the genitalia only. There is sufficient differentiation in the genital structures in both sexes of *Hylobius* to make them useful in separating the species of this genus.

Male Genitalia.—In Coleoptera, the aedeagus (Fig. 36) or male genital tube is composed of sclerites and membranes arranged around the terminal portion of the ejaculatory duct (du. ej.). According to Sharp and Muir (1912) and Snodgrass (1935) the aedeagus belongs to the ninth abdominal segment only. Lindroth and Palmér (1956) divide the sclerites of the aedeagus into two main parts, the penis (p) or median lobe and the tegmen (tm).

The penis (p) is composed of a sclerotized frame surrounded by the first connecting membrane (cm_1) to form a tube containing an internal sac (int. s.). The frame (Fig. 36) is rounded distally and bears a pair of apophyses (apo. p) proximally. The internal sac (int. s.) becomes everted into the female vagina during coitus and is therefore the functional intromittent organ. It is lightly pigmented ventrally (Fig. 36, i) just distal to the tegmen (tm). This pigmented area forms patterns that are constant within species and may be used as a taxonomic characteristic.

The tegmen (tm) is the proximal portion of the aedeagus. It is divided into an unpaired basal piece (bpc) that forms a ring about the penis. It is separated from the freely movable frame of the penis by the first connecting membrane (cm_1) by which it is partially sheathed. Articulating with and distad from the basal piece are a pair of parameres (Fig. 37, pm). The basal piece is produced proximally to form a long apodeme called the manubrium (mab) by Lindroth and Palmér.

Many Coleoptera also have a sclerotized rod (sp) attached ventrally near the apex of the penis. This rod is called a spicule by Sharp and Muir (1912) and a rod or fork by Hopkins (1911). In *H. warreni* it is heavily sclerotized and divided distally into a fork that has a small sclerotized basal plate (Stn 9, bp). This plate is continuous with the membranous sheath of the genital tube. Hopkins (1911) called the prongs of the fork (Fig. 40) a major prong (pr) and a minor prong (pr). These prongs vary in shape and are useful as interspecific taxonomic characters.

Although the eighth abdominal sternite of the male is not considered a genital segment, in this insect it is modified to accommodate the genital organ. It is retracted beneath the seventh tergite when at rest. It is mostly membranous but has two sclerotized areas (Fig. 36, Stn_8) lateral to the apex of the penis which appears to separate them.

Female Genitalia.—As in the male, the eighth abdominal segment is not considered a genital segment but the eighth sternite is frequently modified for the function

	H. warreni	*H. pinicola*
Size	♂ av. 13.2 mm.	Smaller
—length	♀ av. 13.7 mm. av. 13.4 mm. Wood (1957)	av. 12.5 mm. Wood (1957)
Surface	pale-yellow setae, sparse	white setae, more dense
—pronotum	mesal carina short, depressions slight (Fig. 2, Ca)	mesal carina longer, depressions more pronounced (Fig. 3, Ca)
—elytra	apical umbones inconspicuous (Fig. 2, 4)	apical umbones prominent (Fig. 3, 5, Au)
Head		
—frontal fovea	large, deeply impressed (Fig. 9, Fo)	smaller, shallow
—rostrum	long, stout, widening distally (Fig. 9)	long, slender, not widening distally
—antennal scrobe	sharp, hooked (Fig. 17, As)	blunt, straight (Fig. 18, As)
Metanotum	Fig. 21	Fig. 22
—sclerotization	light	heavier
—antecosta	poorly developed, lacks phragma (Ac)	slightly larger, lacks phragma (Ac)
—antecostal suture	straight (acs)	curved (acs)
—anterior membrane	large (mb)	smaller (mb)
—intrascutellar suture	rudimentary (iss_1, iss_2)	prominent (iss_1, iss_2)
—scuto-scutellar suture	rudimentary (vs)	prominent (vs)
—V-shaped ridge	absent	present (VR)
—scutellum	flat (Sct)	raised, bounded by intrascutellar and scuto-scutellar sutures (Sct)
—postnotal plate	rudimentary (PN)	prominent (PN)
Legs	femoral spur inconspicuous or absent (Fig. 28, Fms)	small but present
Hind Wings	vestigial (Fig. 42) venation after Forbes (1922)	fully developed (Fig. 43) venation after Kaston (1936)
—axillary cord	inconspicuous (Fig. 42, AxC)	prominent (Fig. 43, AxC)
Abdomen		
—first two visible segments	median depression large, deeply impressed (variable) (Fig. 26, Stn_3, Stn_4)	median depression small, shallow (variable) (Fig. 27)
Female Genitalia		
—eighth sternite	partly sclerotized to form an apodeme (Fig. 34, apo)	shape of sclerotized area differs (Fig. 35)
—spermatheca	slightly curved (Fig. 32)	hooked (Fig. 33)
Male Genitalia		
—penis	apex rounded (Fig. 36)	apex pointed (Fig. 38)
—tegmen (basal piece) (manubrium)	dorsal margin bisinuate (Fig. 37, bpc) long, slender (Fig. 36, mab)	dorsal margin smoothly rounded (Fig. 39, bpc) shorter, wider (Fig. 38, mab)
—internal sac (median plate)	darkly pigmented, small, sometimes absent (Fig. 36, i)	darkly pigmented, large, always present (Fig. 38, i)
—parameres	long (Fig. 37, pm)	short (Fig. 39, pm)
—spicule (proximal end)	broad and blunt (Fig. 40)	narrow and pointed (Fig. 41)
(prongs)	pointed (Fig. 40, pr)	blunt (Fig. 41, pr)

of reproduction. In *Hylobius* spp. it is lightly sclerotized distally but heavily sclerotized proximally (Fig. 34). The heavily sclerotized area is projected into the body wall as an apodeme (apo).

In Coleoptera the sclerites of the ninth abdominal segment (Fig. 34, cox) are reduced to a pair of "hemisternites", (Lindroth and Palmér, 1956) or "coxites", (Tanner, 1928). Each coxite bears an articulating stylus (st) that is armed with sensory bristles. The vulva (vu) is situated between the coxites and forms the entrance to the genital chamber. This insect also possesses a strongly sclerotized spermatheca (Fig. 32).

All of these sclerotized areas of the female genitalia are useful as interspecific taxonomic characters in *Hylobius* spp.

Differences Between *H. warreni* and *H. pinicola*

These two species are very similar in general appearance and some individuals cannot be identified with certainty unless the hind wings or the genitalia are examined. However, the detailed study of the anatomy has revealed many specific differences, some of which can be ascertained only by dissection. A list of the differences appears on the opposite page.

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Immature Stages, Life Histories, and Behaviour of Two Hymenopterous Parasites of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae)

By J. A. JUILLET

Entomology Research Institute for Biological Control, Research Branch
Canada Department of Agriculture, Belleville, Ontario

Orgilus obscurator (Nees) (Braconidae) and *Temelucha interruptor* (Grav.) (Ichneumonidae), parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), were imported from Europe and released in Waterloo County Reforestation Area, near Elmira, Ontario, from 1955 to 1959.

O. obscurator is the only braconid of known economic importance as a parasite of the shoot moth in Europe (Thorpe, 1930). Recent importations showed that it is also the most abundant parasite of this host throughout Europe. The species was first imported from England in 1928, but was present in Canada earlier (Watson and Arthur, 1959) which suggests an earlier accidental introduction with the host. A total of 8,878 adults were released in Ontario in 1928 to 1949 (Coppel and Arthur, 1954) and 7,912 in 1955 to 1959.

T. interruptor is recorded throughout Europe. Though regarded as a rarity by Thorpe (1930), it was the second most abundant parasite of the shoot moth in recent importations. The species was imported into southern Ontario from England, but was present prior to any release (Watson and Arthur, 1959). A total of 29,998 adults were liberated in 1928 to 1949 (Coppel and Arthur, 1954) and 7,618 in 1955 to 1959.

Materials and Methods

Host larvae were collected at weekly intervals and preserved in 70 per cent alcohol for later dissection. Details of the life histories were secured from host rearings, and adult behaviour was studied as described previously (Juillet, 1959). To work out rates of dispersal, adults were fed an aqueous solution of honey containing radioactive phosphorus (P^{32}) for a few days, released, and recaptured in rotary traps.

Description of Immature Stages

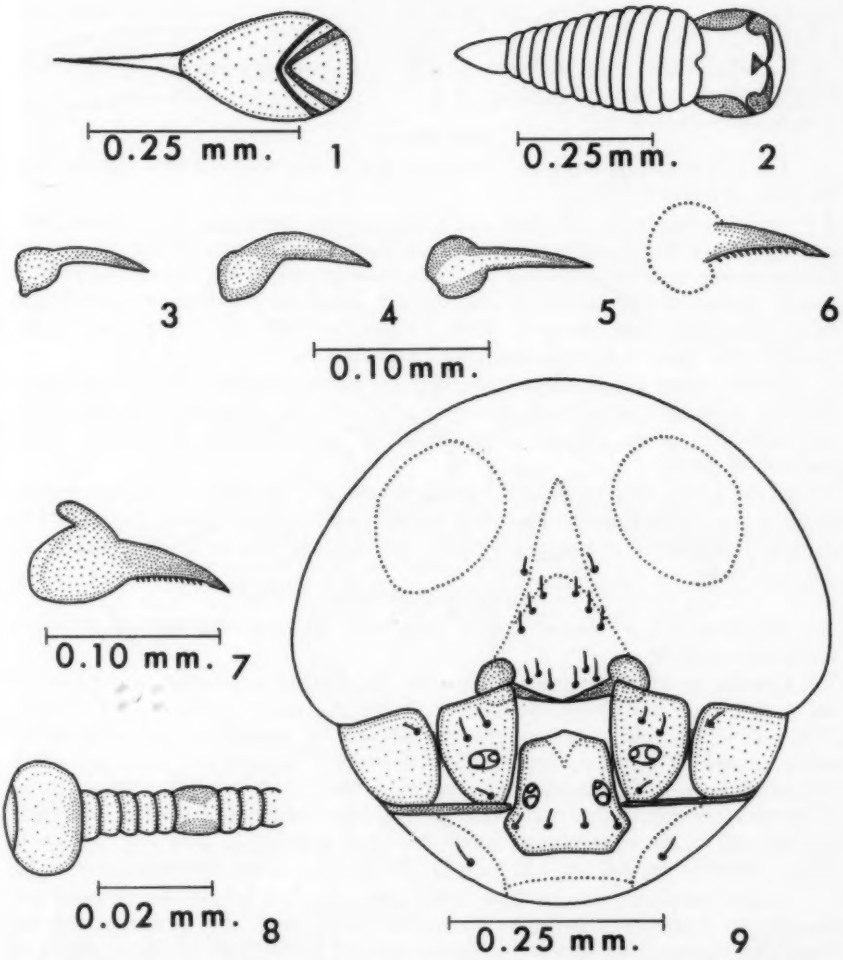
Orgilus obscurator (Nees)

Egg (Fig. 1).—Stalked; chorion smooth, translucent white when first laid, light brown before hatching, and sufficiently hard to retain original shape; two anterior V-shaped sutures ventrally; twice as wide as deep. Increases about five times in size during incubation; before hatching 0.34 mm. long by 0.13 wide.

Larva (Figs. 2 to 9).—Thorpe (1930) briefly described the young and mature larvae and illustrated the cephalic structure of the mature larva as did Short (1952). Mandibular in the first three instars, changing to hymenopteriform in the fourth and fifth; yellowish; 13 body segments; nine pairs of spiracles visible in fifth instar only; cephalic structures strong but simple in first three instars, weak in fourth, well developed in fifth; silk duct, maxillary and labial palpi visible in fifth instar only.

Average measurements in millimeters of the five larval instars, based on five to ten specimens each: first: length 0.58, width 0.22, width of head capsule 0.22; second: 1.15, 0.28, 0.24; third: 2.19, 0.47, 0.31; fourth: 4.55, 0.92, 0.51; fifth: 6.33, 2.17, 0.63.

Cocoon.—Oval, white, densely spun: average size of 10 cocoons: length 6.4 mm., width 2.3 mm.



Figs. 1-9. *O. obscurator*. 1, Egg. 2, First-instar larva. 3-7, Right mandible of larva. 3, First instar. 4, Second instar. 5, Third instar. 6, Fourth instar. 7, Fifth instar. 8, Spiracle of fifth-instar larva. 9, Head capsule of fifth-instar larva.

Temelucha interruptor (Grav.)

Egg (Fig. 10).—Elongate, both ends rounded, curved ventrally; translucent white and uniformly smooth; chorion soft; length 0.17 mm., width 0.06 mm.

Larva (Figs. 11 and 12).—Thorpe (1930) briefly described the young larva and illustrated the cephalic structure of the mature larva as did Beirne (1941). No distinctive differences were observed between the young larva and that of *Eulimneria rufifemur* (Thoms.) (Juillet, 1959) and identification in the early stages is possible only by the dark egg shell of the latter species. The fifth instar is easily differentiated by its cephalic structure.

Average measurements of the five instars, based on three to ten specimens each: first: length 0.99 mm., width 0.10 mm., width of head capsule 0.10 mm.,

second: 1.45, 0.28, 0.17; third: 2.27, 0.42, 0.27; fourth: 4.69, 0.92, 0.73; fifth: 6.81, 1.74, 1.27.

Cocoon.—Oval, light yellow, densely spun; average size of 10 cocoons: length 7.0 mm., width 2.5 mm.

Life History

The life cycles of the two species are similar and are discussed together for the sake of brevity.

Pupation begins in mid-June and adults emerge from late June to late July, starting during the peak emergence of the host. A sex ratio of one to one for *O. obscurator* is consistent with Thorpe's findings (1930), but a ratio of two to one in favour of females for *T. interruptor*, based on recent importations and field emergence data, disagree with Thorpe's record of 62 per cent males. Females live about a month, and males slightly less.

Females mate shortly after emerging and begin oviposition soon thereafter. The egg stage lasts a few days and most of the first instar go into diapause until the following spring, though a few larvae of *O. obscurator* molt once before entering diapause.

In the spring, development is very slow until the host reaches the penultimate or the last larval instar. At that time the parasite develops rapidly and soon kills its host, from which it emerges within a few days to spin its cocoon within the infested shoot.

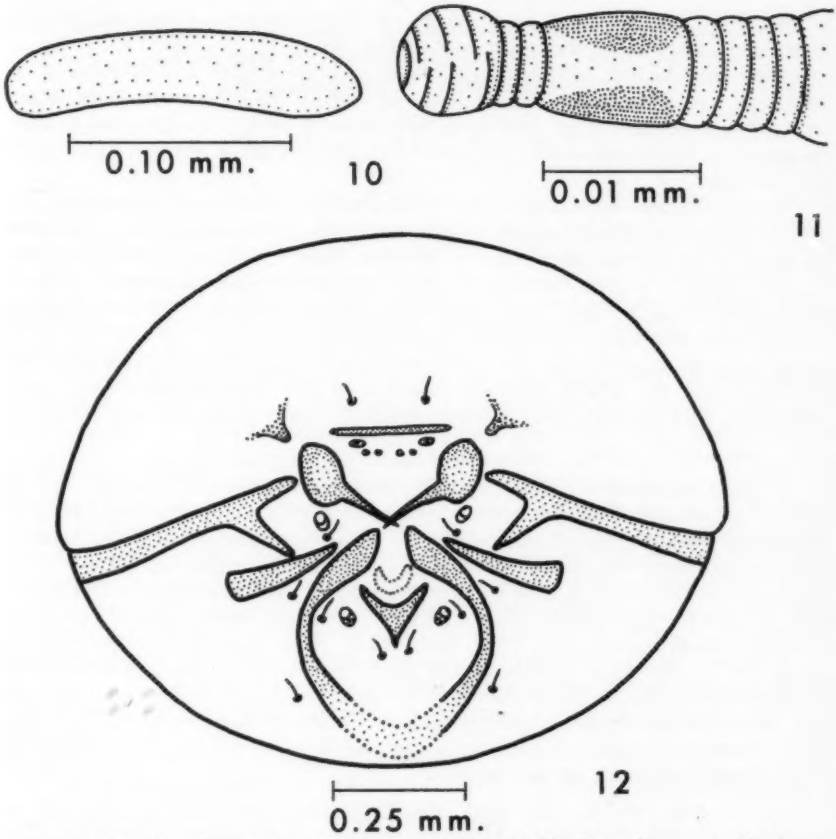
Behaviour of Adult

The behaviour of the two species are similar in many ways and are therefore discussed together.

Copulation.—In both species it usually takes place soon after emergence of the female, but also frequently occurs during the following four or five days. The male of *O. obscurator* mounts the dorsum of the female and vibrates his antennae against those of the female for about a minute and then copulates. Coitus lasts about 45 seconds, but may be as long as 95 seconds. The male of *T. interruptor* approaches the female in a manner similar to that of *E. rufifemur* (Juillet, 1959), but soon mounts her dorsum and copulates. The pair remains in coitus about 45 seconds, and as long as 180 seconds in one instance.

Oviposition.—Attacks by both mated and unmated females occur most frequently on shoot moth larvae in the needle-mining stage, but sometimes on the wandering larvae. All attacks occur on needles within two or three inches of the bud. The female of *O. obscurator* searching for host larvae taps each pair of needles with her antennae, but never probes with her ovipositor in more than one pair. Dissection of 13 of these selected pairs of needles revealed a young shoot moth larva in each. The female often leaves a shoot without probing with her ovipositor and, in all cases observed, these shoots were either uninfested or the young larva had bored into the bud. The female of *T. interruptor* about to oviposit probes with her ovipositor through the sheath of a few needles, apparently at random, and often fails to locate the infested needle.

From the dissection of over 2,000 shoot moth larvae, in no instances was there more than one *O. obscurator* per host. In the same lot of host larvae, *T. interruptor* had laid one or two eggs per host, but in up to 80 per cent of the cases one egg was laid in a host that had already been parasitized by *O. obscurator*. In all instances of multiparasitism *T. interruptor* was the survivor over *O. obscurator*. The frequency of occurrence of the two species in one host is influenced by the percentage parasitism as follows:



Figs. 10-12. *T. interruptor*. 10, Egg. 11, Spiracle of fifth-instar larva. 12, Head capsule of fifth-instar larva.

Years of Collection	*1957*	*1958*
No. *R. buoliana* dissected	1327	1389
O. obscurator (%)	8.4	38.9
T. interruptor (%)	4.3	1.5
T. interruptor and *O. obscurator* (%)	0.5	5.7

Dissection of two freshly-emerged females of both species revealed a reproductive potential of 150 to 200 eggs per female.

Feeding.—In the laboratory, adults of both species fed readily on fresh raisins but preferred an aqueous solution of honey (Leius, in preparation). Leius also found that *O. obscurator* feeds on the inflorescence of Umbelliferae, especially wild parsnip, *Pastinaca sativa* L. Female did not feed on the host larvae. In the field both species often drink dew from the undersides of pine needles.

Flight.—Both species fly during the day only, at temperatures above 55°F. Flight is at its peak between 70° and 80°F. and ceases above 85°F. Wind velocities above five miles per hour do not affect *O. obscurator* which flies very close to the vegetation, but prevent *T. interruptor* from flying except in protected places. *O. obscurator* has a rapid but short flight and darts from branch to

branch about the lower half of the tree. *T. interruptor* has a long and sluggish flight and hovers about the upper half of the tree.

Rate and Pattern of Dispersal.—Males of both species and females of *T. interruptor* have the same rate of dispersal which, for 55 captured specimens, was 165 feet per day at an average temperature of 70°F. At the same average temperature, four females of *O. obscurator* dispersed at an average speed of 84 feet per day.

O. obscurator is not affected by the wind and its pattern of dispersal depends on the density of the surrounding vegetation. The adults always disperse where the shoot moth infestation is more likely to be heavy: in a dense plantation, this is at the edge; in a partly open plantation, it is around the openings. *T. interruptor* flies about the upper half of the tree and the velocity of the wind affects its pattern of dispersal. The adults are carried by the wind when its velocity is above eight miles per hour, seek protected places when it is five to eight miles per hour, and fly in any direction when it is less than five miles per hour. Individuals that remain at low levels to avoid the wind disperse in any direction.

Summary

Orgilus obscurator (Nees) and *Temelucha interruptor* (Grav.) are two internal parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), introduced into Canada from Europe. They overwinter as first-instar larvae and emerge from the mature host larva. There are five larval instars. The longevity of the adults is approximately a month. The immature stages of the two species are described. The adults fly at temperatures of 55° to 85°F. Females usually mate soon after emergence. The reproductive potential is about 150 to 200 eggs. Adults of *O. obscurator* feed on the inflorescence of Umbelliferae. *O. obscurator* flies mainly about the lower half of the tree and *T. interruptor* mainly about the upper half. Males of both species and females of *T. interruptor* disperse at an average rate of 165 feet per day, and females of *O. obscurator* at about 84 feet per day.

Acknowledgments

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Spathimeigenia spinigera Townsend (Diptera: Tachinidae), a Parasite of *Neodiprion swainei* Middleton (Hymenoptera: Tenthredinidae)[1]

By HOWARD A. TRIPP
Forest Biology Laboratory, Quebec, P.Q.

Introduction

The sawfly *Neodiprion swainei* Midd. has long been recognized as a serious defoliator of jack pine, *Pinus banksiana* Lamb., but it was not until the relatively recent use of jack pine as a raw material for pulp that interest in the sawfly became acute. Subsequently, investigations into the natural control of *N. swainei* were begun in the year 1955 near the headwaters of the Gatineau River, P.Q. (47° 55′ N., 75° 25′ W.) which was considered to be near the centre of the current infestation.

The primary object was to study in detail the biology of all the parasites concerned so as to determine their effect on the population dynamics of the host. As the ability to recognize and distinguish their immature stages was of fundamental importance, descriptions of these stages were a natural beginning. This paper deals mainly with descriptions of the immature stages and biology of *Spathimeigenia spinigera* Townsend which was found to be the most abundant parasite in the Clova area. This was the only tachinid parasite found during the present study but, although no difficulty was experienced in distinguishing it from the hymenopterous parasites, other Tachinidae such as *Diplostichus hamatus* (A. & W.) have been recorded from *N. swainei* in the past (Raizenne, 1957). This account of *S. spinigera* should be adequate to distinguish it from *D. hamatus* (*Phorocera hamata*), previously described by Baldwin and Coppel (1949).

It is hoped also that the brief treatise on the taxonomy of the species will serve as a stimulus to some specialist to undertake the much needed revision of the genus.

Taxonomy

The genus *Spathimeigenia* was proposed by Townsend (1915), with *spinigera* as the type species, to replace the name *Admontia demylus* Coq. 1897 (nec *demylus* Walk., 1849). However, no description was given for the species at the time. Aldrich (1931) gave a rather brief description and constructed a key to separate the various species. This is apparently the only key to the species available and despite the accompanying descriptions it is extremely difficult to arrive at exact and definite determinations. Reinhard (1958) drew attention to the difficulties involved with the genus and stated that the colour patterns, chaetotaxy, especially the scutellar bristling, are much too unstable for diagnostic purposes. Until such time as valid taxonomic characters are established for the genus there is little point in attempting detailed descriptions of the adults. For this reason, only the principal key characters of the specimens on hand are given:

Male—Parafrontals and parafacials golden-pollinose. Face, cheeks, and posterior orbit silvery. Parafacials about equal to, or slightly wider than, the width of the third antennal joint. Apex of fourth abdominal segment brownish, especially ventrad. Genital organs brownish. Legs usually black but sometimes brownish, especially the tibiae.

Female—Parafrontals golden-pollinose. Face and parafacials sub-silvery. Cheeks and posterior orbit silvery. Colour of fourth abdominal segment, genitalia, and legs, as in the male.

The original description of *Spathimeigenia aurifrons* Curran (1930) appears to fit that of this species, but in the key of Aldrich (1931) *aurifrons* males are

[1]Contribution No. 582, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

listed as having a parafacial width of less than that of the widest part of the third antennal joint and the females as possessing an entirely black fourth abdominal segment. Dr. C. W. Sabrosky[2] of the U.S. National Museum states that distinctions are not at all satisfactory when working with only keys and descriptions. He finds great difficulty in distinguishing between *Spathimeigenia erecta* Aldrich and *aurifrons* and for the present considers the doubtful northern forms as *erecta-aurifrons* complex. On the other hand, he considers the red-legged southern form to be distinctively *spinigera,* whereas Reinhard (1958), claims *aurifrons* to be closely allied to the type species *spinigera.* I am retaining the specific name *spinigera* for the species under study because I feel that, when sufficient material is made available for comparisons, it will be found that *spinigera, aurifrons,* and perhaps *erecta* are synonymous. For the present, at least, I feel certain that those specimens reared from sawflies in the Provinces of Quebec and Ontario and formerly identified as *aurifrons* are the same as the ones dealt with in this paper. I have arrived at this conclusion on the basis of the similarity between descriptions of the adults and the similarity of the immature stages with those described by Ross (1947) under the name of *aurifrons.* These descriptions agree in all details except that he described the first-instar larva as possessing a single pair of openings to the posterior spiracles whereas these specimens possess bilobate stigmatic chambers to produce four spiracular openings. He also mentions the presence of non-functional anterior spiracles on the second instar. Such spiracles were not encountered in the present study but evidence of the spiracles of the third instar were sometimes noticed on second-instar maggots just prior to the moult.

Distribution and Hosts

During the present study *S. spinigera* has been reared from *N. swainei* from all parts of the Province of Quebec where the sawfly occurs. It is also widely distributed in Ontario (Raizenne, 1957). In the United States it has been recorded by Aldrich (1931) from the New England states, New York, New Jersey, Pennsylvania, Virginia, and Florida. Reinhard (1958) collected it near College Station, Texas.

S. spinigera has also been recorded by Raizenne (1957) as a parasite of *N. rugifrons* Midd., *N. pratti banksianae* Roh., *N. lecontei* (Fitch), *N. pinetum* (Nort.), and *Diprion hercyniae* (Htg.). In addition, Aldrich (1931) includes *N. abbottii* Leach, *N. americanus* Leach, and *N. affinis* Roh. as hosts.

Since *S. aurifrons* is being considered as synonymous with *S. spinigera* in this paper, the following sawflies (Raizenne, 1957) may also be considered as hosts: *Arge pectoralis* (Leach), *Monoctenus fulvus* (Nort.), *Neodiprion abietis* (Harr.), *N. maurus* (Roh.), *Pristiphora erichsonii* (Htg.), and *Pikonema alaskensis* (Roh.). Schedl (1939) reports *S. aurifrons* as an important parasite of *Neodiprion nanulus nanulus* Schedl.

Life Cycle of Host

N. swainei adults emerge in June and July and deposit eggs in the current foliage of jack pine. The eggs are usually placed one per needle and on a single shoot, thus forming an egg cluster which is the product of a single adult. Hatching normally occurs after about one month's incubation and the larvae migrate to and feed as a colony on the previous year's foliage. They pass through four to seven stadia as feeding larvae and then moult to the non-feeding prepupal stage during the latter part of August, September or October. The prepupae leave the colonies and wander over the ground surface in search of suitable places to spin their cocoons in which they pass the winter. Pupation

[2]Personal communication, May 21, 1959.

occurs during May or June and the adult emerges by chewing out the entire apex of its cocoon. Invariably, some larvae fail to pupate the first spring, remaining in a state of diapause until some subsequent year. This provides a reservoir of prepupal larvae in cocoons all the year round.

Description of the Larval Stages of *S. spinigera*

All larval stages are robust and consist of twelve segments including the small and inconspicuous head (procephalon). Each body segment bears minute spines which, in general, are arranged in interrupted rows encompassing each segment near its margin. Otherwise, the cuticle is smooth and transparent.

First Instar—The fully extended first instar is somewhat oval but with a more pronounced taper to the anterior. It is about 1.5 mm. long and 0.7 mm wide at its broadest point.

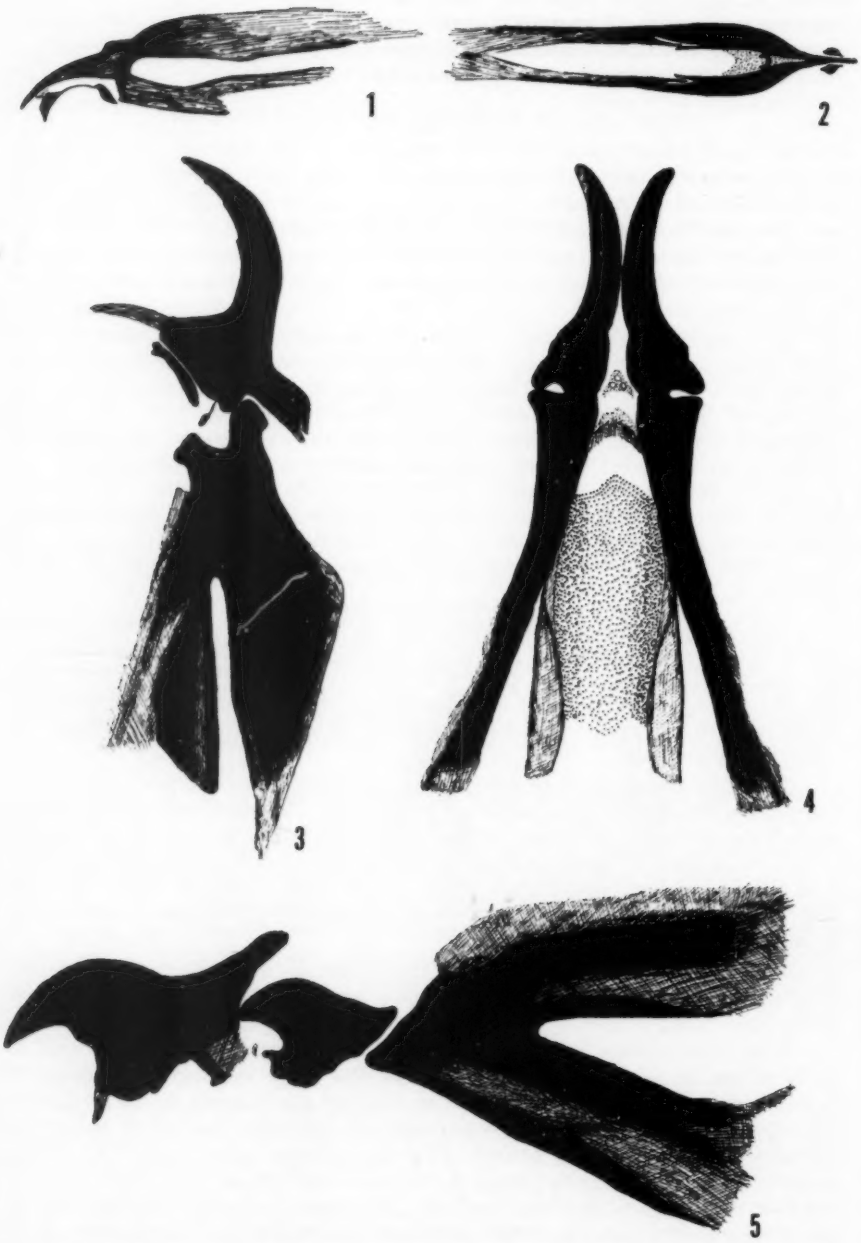
The procephalon is devoid of spines but on the three thoracic and two or three most caudal abdominal segments they are present in bands of five to seven broken rows which completely encircle each segment, being more abundant on the ventral surfaces. Spines on segments three to eight inclusive are almost exclusively confined to the ventral surfaces in two or three rows. Segmentation of the first-instar larva is quite indistinct, making it difficult to ascertain the position of the spines in respect to the margins, but it appears that those on the thoracic segments border the anterior margins and are directed caudad whereas those on the caudal segments are grouped closer to their posterior margins and are directed cephalad. All spines are more or less conical in shape and about .005 mm. long.

The larva is metapneustic, having the spiracles (Fig. 8) situated slightly dorsal on the extreme posterior face of the anal segment. The stigmatic chambers are relatively long and slender and are bilobate near the surface to provide four minute openings. Surrounding the spiracles are three spiracular hooks arranged in the form of a triangle. The most ventral hook is double-pointed whereas the other two are simple.

The most useful characteristic for the identification of the first stage is the form of the buccopharyngeal armature (Figs. 1 and 2), which consists of a single median mouth-hook continuous without articulation with the paired pharyngeal wings. The freshly deposited larva, however, has a lightly sclerotized armature with relatively short pharyngeal wings. The sensory organs (antennae and palps), although inconspicuous, are located on the procephalon just dorsad to the mouth hook.

Second Instar—This stage also tapers to the extremities but is more elongate than the first instar (Fig. 6). It is about 3.0 mm. long and 1.0 mm. wide at its broadest point.

Body segmentation is somewhat more distinct allowing for a more critical study of the spine arrangement. As in the first stage the spines are arranged in bands of irregular and interrupted rows along the margins of the segments. The approximate number of rows per segment and their position in respect to the margins are presented in Table I. There is a general reduction in the number of rows from the extremities toward the mid-abdominal segments as well as an obvious reduction on the dorsal surfaces. On some specimens, however, spines are lacking entirely on the dorsal surfaces of the mid-abdominal segments or if present they are very minute and difficult to detect. The spines along the posterior margins lie close to those on the anterior margins of the adjacent segments. This gives the appearance of four or five dense patches per segment when in fact part of the spines of each patch are on one segment and the



Figs. 1-5. Buccopharyngeal armatures. 1. First instar, lateral view. 2. First instar, ventral view. 3. Second instar, lateral view. 4. Second instar, ventral view. 5. Third instar, lateral view.

TABLE I

The approximate number of rows of spines on the dorsal and ventral regions of the second instar larval segments of *S. spinigera*

Segments	Anterior Margin		Posterior Margin	
	Dorsal	Ventral	Dorsal	Ventral
Procephalon				
I	7	7		
II	9	10		
III	7	10		
IV	6	10		4
V	4	8		7
VI	3	6		9
VII	2	6		10
VIII		5	8	10
IX		3	9	10
X			7	7
XI Scattered spines encircling the spiracular hooks				

remainder on another. Generally the points of the spines on the posterior margins are directed cephalad whereas those on the anterior margins are directed caudad. This is particularly evident at the extremities.

Three types of spines have been recognized (Fig. 10). Acicular spines are common on the posterior margins of the segments and therefore predominate caudally. Those of the conical types are by far the most abundant and predominate cephalad on the anterior margins. The globular types have very short blunt points and for this reason could be termed cuticular nodules rather than spines. They are found in two or three posterior rows ventrally on segments two, three, and four. The largest spines measure only .01 mm. long.

This stage is probably metapneustic in that anterior spiracles could not be detected. The posterior spiracles and spiracular hooks are similar to those of the first stage except that the stigmatic chambers are globose.

The buccopharyngeal armature consists of a pair of slender mouth-hooks which articulate with the paired pharyngeal wings (Fig. 3 and 4). Sensory organs (antennae and palps) may be detected just anterior to the armature on the procephalon.

Third Instar—This stage is elongate, about 6.5 mm. long and 2.0 mm. wide. The spines are less conspicuous than on the second instar. They are less highly pigmented, fewer in number, mostly conical and only very slightly larger. Although the numerous intersegmental folds obscure the arrangement per segment there is no reason to suspect that it differs from that described for the second instar.

The third instar is amphipneustic. The anterior spiracles arise dorsolaterally at the posterior margin of the prothoracic segment and each possesses about 10 papillae (Fig. 9). The posterior spiracles (Fig. 7) are situated slightly dorsad in a shallow depression on the extreme posterior face of the anal segment. They are somewhat triangular in shape and almost contiguous. Each possesses three oval, toothed, respiratory-slits which are slightly elevated from the very heavily sclerotized peritreme. Spiracular hooks are absent.

The buccopharyngeal armature (Fig. 5) consists of a pair of robust sharply curved mouth-hooks which articulate with the conspicuous hypostomal sclerite which in turn articulates with the paired pharyngeal wings.

The Puparium—The puparium (Fig. 11) is subelliptical, about 6.0 mm. long and 2.5 mm. wide at its broadest point. Both ends appear smoothly rounded with a

slight broadening in the ventral-posterior area. The new puparium is yellowish-red but the colour deepens with age to a reddish-brown. The segmentation is distinct but the procephalon of the larva is invaginated and therefore the first apparent segment of the puparium is that of the prothorax. In lateral view the anterior spiracles of the third instar appear as short horn-like protuberances about .85 mm. apart at the extreme anterior of the puparium in a direct line with the longitudinal axis. The posterior spiracles appear as slightly elevated protuberances on the anal segment slightly dorsal to the longitudinal axis. These spiracles, of course, bear no connection with the pupa. Respiration of the pupa is accomplished through the external prothoracic cornicles which protrude through the puparial wall at a point slightly dorsal to the longitudinal axis near the posterior border of the fourth segment of the puparium (Fig. 11). Each cornicle (Fig. 12) is only about 0.1 mm. long, thick-walled, with approximately 12 minute openings at the tip. It leads internally to a broad tracheal trunk which has at its base the internal prothoracic spiracle of the pupa, consisting of about five bilobate processes covered with about one hundred minute papillae.

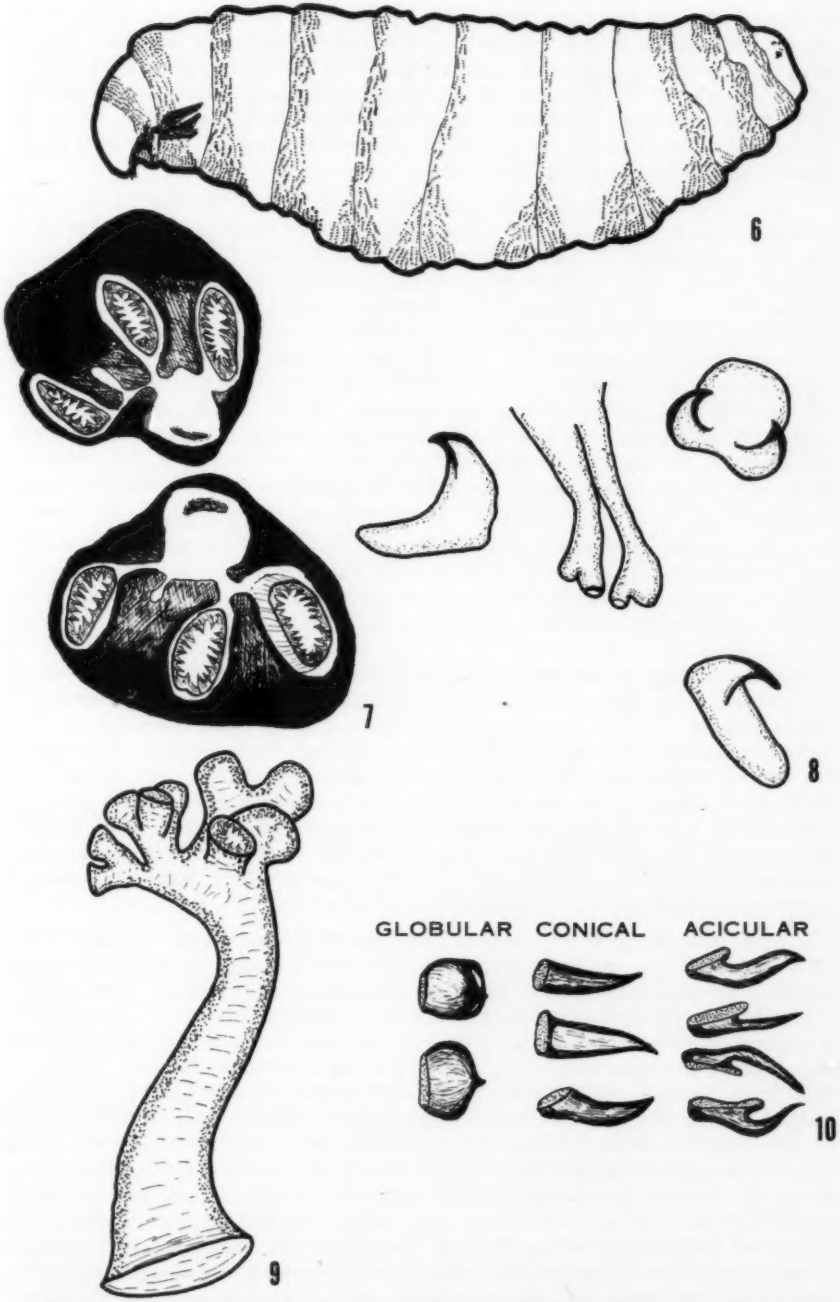
The mouth parts of the third instar are visible through the puparial wall in the ventral thoracic region. The anal opening is represented by a distinct groove at the anterior ventral margin of the last segment.

The horizontal line of cleavage extends directly along the longitudinal axis from the anterior larval spiracles to about mid-way on the fourth segment. The vertical line of cleavage intersects at this point and extends completely around the segment anterior to the cornicles. This results in the puparial cap being divided in half upon the emergence of the adult.

Biology

Emergence of the adults was studied by placing several thousand cocoons in the field under various conditions of ground cover. The male parasites emerged about one week in advance of the females but the sex ratio ultimately reached 1:1 (chi square 0.02). The time and rate of emergence of the host and parasite varied considerably depending on the weather and type of ground cover but under similar conditions the interval between the first appearance of the adult sawflies and parasites was more constant. During 1958, first emergence, from cocoons in more or less exposed areas, occurred on June 23 for the sawflies and July 11 for the parasites (an interval of 20 days). First emergence from cocoons in shaded areas occurred on July 7 and 28 respectively (an interval of 21 days). The period during which the parasites emerged was about 25 days in each case, resulting in freshly emerged parasites being present in the field from July 11 to August 22.

Fecundity is exceedingly difficult to determine, but some estimate may be made through dissection. The internal reproductive system of freshly emerged females (Fig. 13) shows a pair of ovaries each consisting of about 18 ovarioles connected by short oviducts to a short uterus (1.8 mm.). The three spermathecae and two accessory glands lead into the anterior uterus at a point about half a millimetre from the union of the oviducts. The posterior uterus is extremely telescoped but during the following six days it becomes elongated to about 10 times its original length. At this stage the eggs are clearly visible. They lie more or less transversely in a single row at the anterior end but as they progress down the uterus they tend to lie at a slight angle until at the posterior end they are usually in two rows with the head end of each developing egg tilted toward the anterior of the parent. The eggs range from undeveloped at the anterior to fully incubated at the posterior end. The chorions are visible as delicate trans-



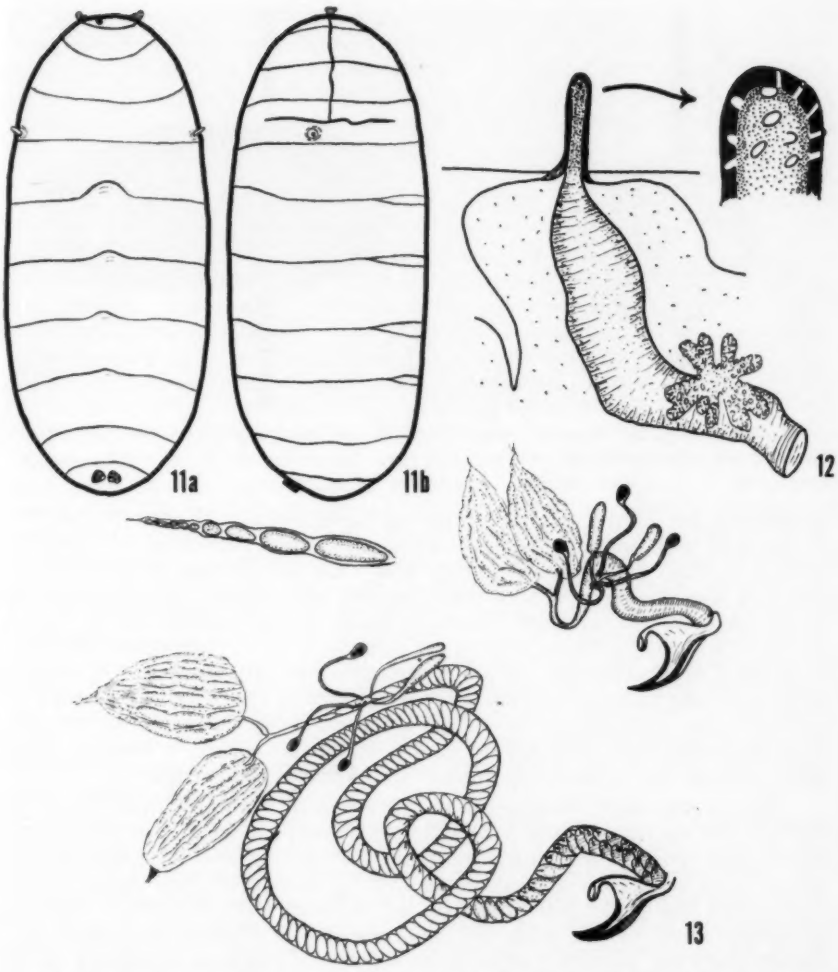
Figs. 6-10. 6. Second instar larva. 7. Posterior spiracles, third instar. 8. Posterior spiracles and hooks, first instar. 9. Anterior spiracle, third instar. 10. Cuticular spines, second instar.

parent membranes but they have never been recovered after deposition of the young. Sometime, during the interval of attack the egg must hatch so it seems safe to classify the species as larviparous. This form of reproductive system would provide for the deposition of larvae over a long period and make an estimate of fecundity extremely difficult as new eggs are probably formed as larvae are born. However, a count of eggs from a gravid female, including those in the ovaries, amounted to approximately 250.

Allowing for the earlier emergence of the male parasites and the pre-larviposition period of the females, fresh gravid females were probably present in the field from about July 24 to near the end of August. This period coincides very well with the presence of suitable host material. Sawfly eggs began hatching on July 23 and the larvae began spinning cocoons during the first week of September. Such synchronization in itself indicates that any larval stage except the prepupae could be attacked. Convincing evidence of this was obtained by exposing colonies of sawfly larvae of different instars in the field for weekly intervals during the months of July and August. When not exposed they were protected and reared in the insectary. Subsequent emergence from these cocoons revealed that successful parasitism occurred on all the feeding stages. No evidence is available in respect to the prepupal stage, but parasitism of this stage is unlikely as the prepupae drop to the ground and crawl through the litter.

The manner of attack is seldom observed because of the speed of the adult and its reluctance to attack when in captivity. The female alights on the foliage or branch a few inches from a colony of larvae. Usually these larvae exhibit the reaction, common to many sawflies, of raising their heads in unison and exuding from the mouth a ball of sticky substance. Whether this is primarily a defensive reaction against parasitism is uncertain but, in any event, it does have a dire effect on some of the hymenopterous parasites by gumming-up the ovipositor. In the case of *spinigera* this has never been observed but it is entirely possible. During a lull in the host reaction, the fly darts in, flicks across the colony and departs from the immediate vicinity with such speed that it is difficult to follow its movement. However, the evidence of the attack becomes immediately apparent by the presence of a small ball of body fluid exuding through the cuticle of one host, usually dorsally in the thoracic region. Immediate dissection of this larva reveals the presence of a first-instar maggot lying just beneath the cuticle at the point of puncture.

First-instar maggots may be located almost anywhere within the body cavity of the host. They do not appear to be associated with any particular organ unless it be the ribbon-like fat body in which they are frequently enshrouded. Careful dissection of the host reveals that these tiny maggots become attached to a tracheal trunk by their caudal ends and that they are apparently held in place by means of the spiracular hooks. Such a mode of respiration would require at least some modification at each moult of the host. After the host reaches the prepupal stage and spins its cocoon, the maggot becomes attached to the integument, where the familiar respiratory cup is formed. The respiratory cup or scar may be located almost anywhere on the host body, but not on the head; however, it is more frequently encountered ventrally in the thoracic region. In all cases after the cup has been formed the maggot has been found in the second instar but the position of the moulted skin about the posterior of the maggot clearly shows that the original attachment to the cuticle was established by the first instar. In addition to the respiratory cup, a membranous opaque sheath is formed which surrounds the posterior half or more of the parasite. The parasite is held in place in the cup by means of its spiracular hooks and within the sheath



Figs. 11-13. 11. Puparium, dorsal and lateral views. 12. Puparial cornicle and internal spiracle of pupa. 13. Internal reproductive systems of immature and gravid female adults with diagram of a single ovariole.

as a result of the anteriorly directed spines on the posterior segments. Although both the respiratory cup and the sheath are of host origin they do not appear to be otherwise associated. The respiratory cup appears as an extension of the cuticle and may be the result of a healing process. Mechanical injury to the prepupae resulting from the oviposition by other parasites, namely *Exenterus canadensis* Prov., brings about a darkening or scarring of the cuticle which is similar to the scar about the respiratory opening. The formation of the sheath appears to be a different process, in that it is also present when the larva is attached to the trachea.

The majority of specimens pass the winter in the first stadium, but occasionally a second-instar maggot is discovered in hibernation. After moulting

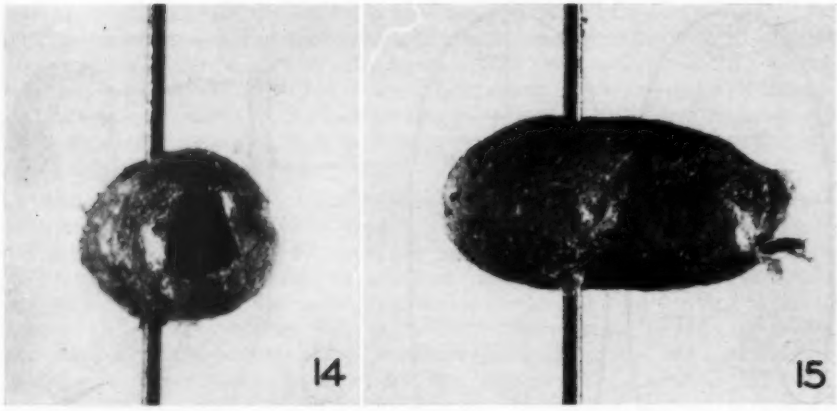


Fig. 14. *N. swainei* cocoon showing emergence hole made by the parasite, *S. spinigera*. Fig. 15. Same as above, lateral view.

to the third stadium the respiratory opening is abandoned. The third-instar larva is equipped with anterior spiracles and apparently respiration is accomplished directly through the integument of the host. Up to this stage the host remains alive but once the third stadium is reached the host dies and its body contents become more or less liquefied. Soon the entire contents, except the silk glands and the ectodermal digestive system, are consumed. The fully developed third-instar larva breaks through the host integument and proceeds to make the exit hole in the host cocoon to facilitate the emergence of the adult. It would seem from the appearance of the cocoon that this is accomplished by the larva rasping with the mouth hooks until the entire end of the host cocoon is worn to tissue-paper thinness and a small hole appears in the centre of the area.

Shortly thereafter, the puparium is formed with the anterior end facing the exit hole and the host remains lying full length along one side. Upon emergence of the adult the puparium cracks along the cleavage lines to form two cap-like pieces which usually do not become completely disengaged from the rest of the puparium. The adult then protrudes the ptilinum through the tiny opening previously made by the larva and by expanding and contracting this organ literally tears the weakened edges of the cocoon. The final emergence of the adult from the host cocoon forces the torn edges outward resulting in an emergence hole as shown in Figures 14 and 15.

Although there is typically one generation per year, a few larvae do not develop past the second instar during the first year but remain in a state of diapause completing their development the following year or later.

Mortality Factors

There are at least five major factors that tend to decrease the effectiveness of this parasite, namely superparasitism, encapsulation, multiparasitism, diapause, and effect on host development. Because of their individual significance, the subjects of superparasitism and encapsulation will be treated in publications to follow. In the meantime, it suffices to state that superparasitism is rather common and is certainly a limiting factor, for only a single maggot may develop to the adult stage from a single host larva. Encapsulation of parasites is a phenomenon which is by no means confined to *S. spinigera* but which seems equally effective on all

the internal parasites of *N. swainei*. Briefly, the process appears to be the formation of a gelatinous material which encases the immature stages of the parasites. Eventually, this material darkens and hardens to trap and destroy the parasite. Such encapsulated parasites are often found in adult sawflies.

Multiparasitism—The occurrence of other parasites in the same individual host often results in the death of the tachinid larvae either through competition for host material or as a result of accidental hyperparasitism. Many parasites of *N. swainei* feed externally on the sawfly larva within its cocoon and in so doing destroy the endoparasitic tachinid larva. One of these is *Exenterus canadensis* Prov., which deposits its eggs externally on the prepupa. After the sawfly spins its cocoon the egg hatches and the larva develops as an ectoparasite within the host cocoon. Dissection of cocoons from which *E. canadensis* have emerged often reveals the remains of tachinid larvae. Since *spinigera* is so abundant (often parasitizing up to 70 per cent of the population in some areas), the chances of such encounters are quite common. The effect of *E. canadensis* was demonstrated by exposing a sample of *N. swainei* to the attacks of this parasite and comparing the emergence against a similar sample that was not so exposed. The unexposed sample produced 43 per cent *spinigera* as compared with 30 per cent from those exposed, the difference apparently due to the chance encounters between the two species. Similar mortality may result to *spinigera* through the competition of other ectoparasites, namely *Endasys subclavatus* (Say), *Aptesis indistincta* (Prov.), *Mastrus argeae* (Vier.), and *Dahlbominus fuliginosus* (Nees). All these parasites deposit their eggs through the sawfly cocoon externally on the host larva and they may undergo several generations each year as a result of the continual presence of such host material. In a few instances the adults of *A. indistincta* and *M. argeae* may attack a specimen containing *S. spinigera* in an advanced stage of development. When this occurs, these parasites may develop hyperparasitically, as evidenced by the presence of their particular cocoons within the puparia of *S. spinigera*. Still another parasite, *Perilampus hyalinus* Say, has been found to be hyperparasitic on *S. spinigera*, but it may develop successfully in the absence of the tachinid.

Despite the obvious inferiority of *S. spinigera* to others on *N. swainei*, it still remains the most abundant parasite in the area under intensive study. The situation, however, is quite different in some of the other infested areas. For example, in the Lake St. John area in 1957, *S. spinigera* represented only 2.5 per cent of the total emergence while *A. indistincta* constituted 23.2 per cent. On the other hand, *A. indistincta* was an extremely uncommon parasite in the Gatineau area, accounting for only 2.1 per cent of the total emergence as against 34.0 per cent for *S. spinigera*. The total percentage parasitism, however, in each area was approximately the same.

The matter of parasite relationships is extremely complex and any attempt to explain the differences in the population levels must be highly speculative. Apparently *S. spinigera* can thrive only when certain other parasites are at an endemic level. Nevertheless, it is capable of reproducing at a very rapid rate and must be considered as an important natural control factor.

Diapause—Each year a certain percentage of sawfly larvae in cocoons remain in a state of diapause throughout the summer and resume development in the next or subsequent years. In this manner, there is always a reservoir of sawfly larvae in the soil and the adult sawflies for any given year are derived from several generations. Although a few of the specimens in extended diapause may contain parasites which like the host remain in a state of diapause for an indefinite number of years, it has been found that there is a much greater tendency for the parasites

TABLE II
Relative emergence of *N. swainei* and its parasite, *S. spinigera*, after one and two periods of hibernation

	N. swainei		*S. spinigera*	
	No.	Per cent	No.	Per cent
Non diapause One hibernation period	435	43.1	575	56.9
Diapause Two hibernation periods	198	91.3	19	8.7

to complete their development in one year (Table II). It follows, then, that any mortality factor, such as unfavourable weather conditions, affecting the feeding host larvae and parasites alike would be more detrimental to the parasite. That is, if the sawfly larvae of a given season are destroyed, the succeeding generation must necessarily be derived from the reservoir of diapause larvae which in turn are likely to be relatively free of the parasite. In this way, the phenomenon of diapause has an indirect bearing on the population dynamics of *S. spinigera*.

Effect on Development—Hosts containing *S. spinigera* parasites develop more slowly than those that are unparasitized. During 1955, a sample of sawfly larvae were collected during early August and subsequently reared in an insectary protected against further parasitism. The spinning dates of each host were recorded and it was found that those maturing early contained fewer parasites than those maturing later (Table III). Normally, the spinning of cocoons begins

TABLE III
Spinning dates of *N. swainei* larvae in respect to parasitism by *S. spinigera*

Date of spinning	Unparasitized	Parasitized	Per cent parasitism
Prior to August 18	161	40	19.9
August 18 to August 22	80	31	28.0
After August 22	31	50	61.7
Total	272	121	30.8

around the first of September[3], reaches a peak about mid-September and continues on into late October. Quite often, however, the weather conditions become unfavourable for further development during September and only those that reach the cocoon stage by early September manage to survive. It follows, then, that the parasite suffers more from such unfavourable conditions than does the host.

Summary

Spathimeigenia spinigera Townsend (Tachinidae) is a native parasite common in the eastern parts of North America on many species of sawflies, particularly *Neodiprion swainei* Middleton, on which the present study was conducted. The identification of the species within the genus *Spathimeigenia* is extremely difficult in that the specific characters being employed are too variable. In this paper the species *S. aurifrons* is considered synonymous with *S. spinigera* because the detailed descriptions of the immature stages presented here are sufficiently similar to those presented for *S. aurifrons* (Ross, 1947) to warrant this conclusion.

S. spinigera may attack any larval stage of the host except the prepupae. The young are deposited directly into the body cavity as first-instar maggots

[3]The summer of 1955 was abnormally hot and dry and the development of the sawflies extremely rapid.

which become attached to a tracheal trunk and held in place by means of posterior spiracular hooks. After hibernation and before the moult to the second instar they become attached in a similar manner to the host body wall where an integumental respiratory cup of host origin is formed. The third-instar maggots, however, abandon this attachment and proceed to break down the tissues of the host until practically all the internal contents have been consumed. The puparium is formed within the host cocoon and the adult emerges through a hole made by the third-instar maggot.

Factors which tend to decrease the effectiveness of the parasite, namely superparasitism, multiparasitism, encapsulation, diapause, and effect on host development, are discussed.

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A Polyhedrosis Virus and a Microsporidian Disease of *Aletia oxygala luteopallens* (Sm.) (Lepidoptera: Noctuidae)[1]

By W. A. SMIRNOFF
Forest Biology Laboratory, Quebec, P.Q.

Larvae of *Aletia oxygala luteopallens* (Sm.)[2] found on chicory (*Cichorium intybus* L.) in Quebec City in May, 1958, were infested with a nuclear polyhedrosis virus and with a microsporidian. Larvae suffering from polyhedrosis leave the interior of the stems, die, and remain hanging in a characteristic way "glued" to the exterior of stems. The diagnosis of the polyhedrosis virus was confirmed by Dr. G. H. Bergold at the Insect Pathology Research Institute at Sault Ste. Marie, Ontario, and that of the microsporidian by Dr. H. M. Thomson of the same Institute. Neither microorganism had ever been noticed before.

The larvae of *A. o. luteopallens* live a nocturnal life, leaving the stem of the chicory at night to feed on surrounding plants, predominantly grasses and sedges. In the morning they return to broken stems of chicory but not necessarily the same ones. They were infected with the polyhedrosis virus by dipping their heads in a heavy aqueous suspension of polyhedra. After four to six days, they turned from a yellow-green to a milky-cream colour and died from polyhedrosis in 10 to 12 days. The polyhedra were large, measuring four to six microns in diameter.

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[1]Contribution No. 613, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

[2]Identification of the larvae was made by Dr. S. E. Crumb, Agricultural Research Service, Beltsville, Maryland, U.S.A.

A Review of the Life-History and Habits of *Musca autumnalis* DeGeer (Diptera: Muscidae)

By H. J. Teskey

Entomology Laboratory, Research Branch
Canada Department of Agriculture, Guelph, Ontario

It was of interest but no great concern when the finding of *Musca autumnalis* DeGeer in Nova Scotia was reported by Vockeroth (1953). Previously, *M. domestica* Linnaeus was thought to be the only species of the genus present in North America. Two previous reports of *M. autumnalis* as *corvina* (Walker, 1849, 1871) were thought to be misidentifications.

The presence of *M. autumnalis* in North America is now causing much concern. The species has been reported from Prince Edward Island, Nova Scotia, New Brunswick, Quebec, and Ontario in Canada, and from Vermont, New Hampshire, Delaware, New Jersey, New York, Massachusetts, Pennsylvania, West Virginia, Virginia, Ohio, Michigan, Minnesota, Iowa, Indiana, and Illinois in the United States (MacNay, 1957, 1958; Agr. Res. Serv. 1959). Many of the reports made since 1957 noted that the species was abundant enough on cattle to cause the animals noticeable discomfort. Densities of from 30 to 50 flies per animal have been reported from Ontario, Ohio, Illinois, and Indiana. In Ohio, it was stated to be the most annoying fly on cattle in 1959 and to have caused possible decreases in milk production (Agr. Res. Serv. 1959, p. 737).

The rapid rise of *M. autumnalis* to prominence in eastern North America will undoubtedly prompt research on this pest. This is a review of the literature on *M. autumnalis*, along with some of the writer's observations.

The Genus *Musca*

The genus *Musca* comprises 51 valid species of polyphagous and haematophagous flies, the immature stages of which are spent in or near animal excrement and garbage of various kinds (West, 1951). The majority of these species are confined to the Palaearctic, Ethiopian, and Oriental regions.

Two approaches have been employed in the development of the classification of the genus *Musca*. Malloch (1925, 1929) and Townsend (1915, 1921) made use chiefly of the chaetotaxy, whereas, Patton (1932, 1933, 1933b, 1936, 1937) stressed the structure of the genitalia as well as various biological differences. The two systems were harmonized by van Emden (1939). The identification and distribution of the species *Musca* were satisfactorily dealt with in papers by Patton (1933, 1936, 1937) and van Emden (1939).

Vockeroth (1953) has pointed out the difficulty in identifying *M. autumnalis* to genera in Curran's (1934) key to North American Muscidae. Patton (1933) reported that a basal grapelike sensorium in the third antennal segment, opening by a duct into the socket, was an important generic character of *Musca*.

Musca autumnalis DeGeer

The synonyms of *M. autumnalis*, as given by West (1951) include: *continua* R.D.; *corvina* Port.; *floralis* R.D.; *grisella* R.D.; *ludifacies* R.D.; *nigripes* Panz.; *ovipora* Port.; *prashadii* Patton; *rustica* R.D.; and *tau* Schrank. Four subspecies of *M. autumnalis* have been described: *autumnalis* DeGeer, *pseudocorvina* van E., *somalorum* Bezzi, and *ugandae* van E. The typical subspecies is the form found in most of the Palaeoarctic region and at present causing concern in North America. The other three subspecies appear to be confined to the Ethiopian region.

West (1951) and Patton (1933) reported that the typical subspecies was found from Shantung and Kashmir to Palestine, North Africa, and Europe. In addition, it was reported from Korea by Okamota (1924). Froggatt (1917) found *M. autumnalis* (as *corvina*) as prey of wasps in Australia; since no other report of the presence of the species in Australia was found, the validity of the identification is in doubt.

Descriptions

The following descriptions of *M. autumnalis* are condensed from Patton (1933b) and van Emden (1939). The descriptions of the adults are sufficient to separate them from other known species of *Musca.*

Male

Head–Eyes bare and separated above by less than the width of the ocellar triangle; lower part of vertex silvery, cheeks white.

Thorax–Mesonotum ground colour bluish-grey, lightly pollinose, with four broad black stripes; propleura bare in the depression between the humeral callus and the propleural bristles; thoracic hair fine and long, from one and a half to twice as long as width of third antennal segment; suprasquamal ridge with bristly hairs on lower front extremity; two to four bristles on posterior side of dorsal surface of stem vein; setulae on ventral surface of vein R 4+5 confined to base, not reaching R-M.

Abdomen–Dark orange with a reddish tinge; dorsum of terga 1+2 black, lateral regions orange; terga 3 and 4 dark orange with a broad median black stripe expanding anteriorly on tergum 3 and posteriorly on tergum 4; tergum 5 dark in middle, antero-lateral margins orange; sterna 1+2 and distal end of 5 light to dark brown; sterna 3 and 4 orange.

An illustrated description of the male genitalia was given by Patton (1933).

Female

Head–Vertex wide, almost the width of an eye; orbital stripe grey pollinose, at least half as wide as the black median frontal stripe; outer vertical bristles strong and arranged somewhat irregularly in two rows; cheeks grey.

Thorax–Mesonotum ground colour slate grey with four broad black stripes; chaetotaxy as in the male.

Abdomen–Ground colour black; anterior ventro-lateral region of terga 1 + 2 orange yellow; terga 3 and 4 with a narrow median black stripe, remainder silvery grey irridescent spots; sterna black pollinose.

Egg

The eggs are distinctive because of the long greyish-black mast or stalk projecting from one end. The egg itself is yellowish white without any visible chorion sculpture. Including the mast, the egg is about 3.1 mm. long and 0.5 mm. broad. The mast is about 0.7 mm. long and 0.1 mm. broad, grooved on the dorsal side and generally somewhat curved at the tip. Two ridges run along the dorsal side of the egg and are continuous with the edges of the groove on the mast.

Larvae

The mature third-stage larva is similar in size and shape to the house-fly larva. The anterior spiracles bear eight to nine finger-like openings. The posterior spiracles are D-shaped, with the straight inner margins more closely approximated below than above. The spiracular plates are densely chitinized and lack a distinct peritreme. The three sinuous spiracular slits are relatively short and narrow.

The spiracles are separated by about one quarter the width of a plate. The full grown larva is a characteristic yellowish colour.

Pupa

The pupa is similar in size and shape to the house-fly pupa. The most striking difference is the dirty-white, almost transparent colour of the pupa of *M. autumnalis*.

Comparison of adults of *Musca autumnalis* and *M. domestica*

M. autumnalis and *M. domestica* may be separated in both sexes by the absence and presence, respectively, of hair on the propleuron. The eyes of the male are almost touching in *M. autumnalis* and well separated in *M. domestica*. The female of *M. autumnalis* has the dorsum of the abdomen entirely silvery black and the orbital stripes grey, each at least half as wide as the median frontal stripe. The dorsum of the abdomen in the female of *M. domestica* is usually yellowish at the sides and the yellowish-tinted orbital stripes are each about one-third as wide as the median frontal stripe.

Life-History and Habits

The life-history and habits of *M. autumnalis* have received little attention. Many of the papers in which the species is mentioned refer only to the haematophagous feeding habit of the adults and to the dung habitat of the larvae. The most extensive study has been reported by Hammer (1942) from Denmark.

Hammer considers that *M. autumnalis* is one of a group of flies that are in transition between general secretion suckers and blood suckers. He reported that *M. autumnalis* fed on the nectar of a wide variety of flowers and believed that nectar was the principal diet of the flies in the spring before cattle were pastured. Hammer (1942) and Derbeneva-Ukhova (1942) frequently observed *M. autumnalis* feeding on fluids on the surface of dung. The latter author, referring to the relationship between egg maturation and nutrition of a number of dung flies, considered *M. autumnalis* as a facultative blood feeder that could obtain its nitrogenous materials for egg maturation from dung as well as from blood. The feeding habit most frequently reported and which resulted in the species being considered as such a pest of cattle was that of feeding on the various secretions from the animal. Because the eyes and the muzzle offer the most constant source of such secretions the flies are most frequently noted there. When seen on the body they are frequently feeding on the strings of saliva thrown there when the animal tries to dislodge horn flies, or on the blood or discharge exuding from wounds made by the bites of tabanids or by other injuries.

The peculiar trait of feeding on the blood exuding from wounds made by biting flies has been observed frequently (Derbeneva-Ukhova, 1940; Hammer, 1942; Thomsen, 1938; Patton, 1933b). Although tabanids are mentioned most frequently as serving the meal, Thomsen (1938) observed *autumnalis* to imbibe blood left by *Stomoxys, Haematobia* and *Lyperosia* spp. Hammer (1942) noted as many as 30 *autumnalis* clustered around a feeding horse fly waiting for it to depart. Frequently, they forced the horse fly to leave unengorged.

The stimuli that attract *M. autumnalis* to its hosts are unknown. Hammer (1942) considered odour to be the major attractant. He observed, on several occasions, that *M. autumnalis* left a cow to attempt feeding on blood exuding from a fresh scratch on his hand. The writer has noted himself to be attractive to feeding females of *M. autumnalis* when he was perspiring heavily.

Hammer (1942) found *M. autumnalis* feeding on cattle only during the daylight hours and most abundantly on cattle near woods, game coverts, swampy

areas, and many hedgerows. During the night, the flies rested on vegetation. He attributed their abundance in the above situations to be related to the abundance of biting flies in such localities, from whose bites *M. autumnalis* obtains much of its blood. Male flies were seldom noted on cattle.

In Europe, the flies are present in the field from May to October (Graham-Smith, 1916; Hammer, 1942). The writer has found the same seasonal occurrence on cattle in Ontario with the species being most abundant during the first half of August in 1957 and 1958. Hammer noted the seasonal occurrence of the flies to be characterized by a series of peaks in abundance that he attributed to mass hatching of generations.

Conspicuous objects in the field, such as a lonely bush, a rock, a cow, or a cart, are believed to be the sites of mating (Hammer, 1942). Hammer observed males resting on such objects to dart out and attach themselves to females that were flying past. The pairs dropped to the ground to complete mating.

Derbeneva-Ukhova (1942) studied the process of maturation of the ovaries in *M. autumnalis* and 14 other species of dung flies. He considered that the seven stages in ovarian development distinguished by Christophers (1940) and Mer (1936) were applicable to the flies studied. He showed that on the basis of oviposition habits, three groups of dung flies existed. *M. autumnalis* belongs to the group in which the eggs are laid at different times, though all are matured together.

The larvae of *M. autumnalis* develop in isolated patches of dung dropped in the field (Hammer, 1942; Patton, 1933). Vainshtein and Rodova (1940) found the larvae in both cow and pig dung. Kobayashi (1919) reported that, in Seoul, *M. autumnalis* oviposited in latrines.

Hammer (1942) noted that gravid females of *M. autumnalis* began arriving at patches of cow dung within a minute after it was dropped. Maximum oviposition occurred within twenty minutes after the dung had been dropped. A few flies appeared on dung up to 24 hours old. The female flies crept over the surface of the dung and laid their eggs one at a time, usually in places where the surface was smooth. Frequently, batches of five to eight eggs were laid close together. When the flies were abundant, several hundred eggs per dropping were noted.

Although confirming Hammer's report in most details, the author observed that cow dung lost its attractiveness for ovipositing flies within an hour of deposition. This appeared to be related to the rapidity of the development of a crust over the surface of the dropping. Flies arriving at fresh dung laid their eggs indiscriminately in the surface. As the dung aged, flies were apparently unable to penetrate the thin crust with the ovipositor and deposited their eggs in small pits and crevices in the surface of the dung where the accumulated moisture had delayed drying and hardening. It was in such sites that clusters of eggs were found. Flies were not observed to lay their full complements of eggs in one patch of dung.

Portchinsky (1885), reviewed by Osten Sacken (1887), stated that *M. autumnalis* laid 24 eggs. Hammer (1942) found an average of 24.6 eggs and as many as 31 eggs per female in the ovaries. The writer noted similar variation in the number of eggs per female.

Several authors, including West (1951), refer to the mast as a stalk by which the egg is attached to the dung. The eggs, however, are deposited in the same position they are present in the ovary, that is, with the mast upwards. Hammer

(1942) observed the survival of eggs variously sealed with paraffin and concluded that the mast was a respiratory structure and must be exposed to air for survival of the egg.

In Denmark, Hammer found average incubation periods of 10½ and 23 hours for eggs laid in dung in the mornings and afternoons, respectively. At air temperature not exceeding 80° F. incubation periods of less than 21 hours were observed by the writer for eggs laid in fresh cow dung.

Little is known of the movements of the newly hatched larvae or of the relationship of the structure and composition of cow dung to the survival and development of the larvae. Many other insects occur in cow dung with the larvae of *M. autumnalis*. Hammer (1942) found 64 species of flies associated with cattle droppings in Denmark and gave references to several more. He found that these insects, by predation and modification of the physical structure of the environment, adversely affected the survival of *M. autumnalis*.

The writer has found, on evidence of the increase in size of the cephalopharyngeal skeleton, that the larvae of *M. autumnalis* pass through three stages. The growth of the larvae was rapid, requiring 2½ days in larvae reared in the laboratory at approximately 75° F. Three to four days were required for larvae to complete their development in droppings in the field.

The mature larvae pupate near the edge of a dropping or in the soil surrounding it. Hammer (1942) noted larvae emigrating from droppings just before sunrise. He found only one puparium in the field and this at the bottom and near the edge of a dropping. The writer has found puparia under approximately a quarter inch of soil within a few inches of droppings. The duration of the pupal period was seven days in pupae reared in the laboratory at 75° F., and ten days in the field. Development from egg to adult required approximately three weeks in Denmark (Hammer, 1942) and about two weeks in Ontario.

Large numbers of *M. autumnalis* have been reported to hibernate in houses (Eltringham, 1916; Graham-Smith, 1918; Hammer, 1942; Kearns, 1942; and Reh, 1927). It was this habit that first drew attention to the fly in North America (Vockeroth, 1953). It is apparently the annoyance caused during hibernation that is of greatest concern in Great Britain, for the literature on *M. autumnalis* from that country refers almost exclusive to this habit. Hammer (1942) found no adults hibernating in the field. He suggested that they do so, in cracks and crevices in the bark of trees and elsewhere, because he observed large numbers of flies on cattle grazing near woods in the spring, whereas few flies were present on cattle in open pastures.

Roubaud (1927) concluded that the hibernating forms of *M. autumnalis* were fertilized females in which ovarian development was suspended for several months, whether they fed or not. Hammer (1942), however, found hibernating females with spermathecae empty and undeveloped ovaries.

Predators and Parasites

Much has been written of the predators and parasites of house flies and related species (West, 1951). Only a few of these are known to affect *M. autumnalis*. Hammer (1942) listed several predators and parasites of the fauna in or on cattle droppings. Of these, only species of the hymenopteran genera *Vespa* and *Mellinus* and the parasitic fungus *Empusa* were mentioned as attacking *M. autumnalis*. Sabrosky (1956) reported finding *M. autumnalis* in a nest of *Bembis pruinosa* (Fox).

M. autumnalis as a Disease and Parasite Vector

Several workers have suggested that *M. autumnalis* may transmit certain disease organisms and have urged that greater attention be paid the species in this regard (Mercier, 1925; Patton and Cragg, 1913). However, it has not been shown to be the vector of any disease. Lamborn (1937) suggested that the disappearance of leprosy in Europe may have resulted from the control of *M. autumnalis* and other haematophagous flies by the introduction of modern methods of sanitation. He pointed out that *M. autumnalis* is similar in habits to *M. sorbens* Wied., a known vector of the disease. Because of the fly's habit of feeding on secretions from the various orifices of the bodies of cattle, it has been suggested that *M. autumnalis* may transmit infectious abortion (Hammer, 1942) and pink eye, or conjunctivitis (Thomsen, 1938). Klesov (1949) found that *M. autumnalis* was an intermediate host of a mammalian eye worm, *Thelazia rhodesi* Desmarest, prevalent in Russia. Sabrosky (1959b) suggested that, in the event of *M. autumnalis* extending its range to the west coast, it may serve as a host for an American species of eye worm, *Thelazia californiensis*. Stephens (1905) reported a human case of intestinal myiasis caused by *M. autumnalis*.

Summary

The adult of *M. autumnalis* DeG. is a facultative blood sucker, mainly of cattle. It feeds on nectar, secretions from animals, and dung liquids. In addition to the annoyance caused cattle, the flies are suspected to be vectors of certain diseases, but no proof of this has been presented. The fly is present in the field throughout the summer, entering buildings only to hibernate. The eggs are laid singly in patches of fresh cattle dung dropped in the pasture. The coprophagous larvae develop rapidly through three instars and pupate near the edges of the droppings. Developmental time from egg to adult is about two weeks in southwestern Ontario.

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Myzus certus (Wlk.), an Efficient Vector of Potato Virus Y[1]

By M. E. MacGillivray and R. H. E. Bradley
Entomology and Plant Pathology Section, Research Station, Research Branch
Canada Department of Agriculture, Fredericton, N.B.

There seems to be only one report of the aphid *Myzus certus* (Wlk.) transmitting a virus, bean yellow mosaic virus (Swenson, 1957). It is therefore noteworthy that *M. certus* transmits potato virus Y as readily as does *Myzus persicae* (Sulz.), until now the most efficient vector known for virus Y. In one experiment that showed this, the numbers of single aphids out of 50 that transmitted virus Y were 27 and 28 respectively. Briefly the experiment was as follows: *M. certus* was reared on pansy (*Viola tricolor*) and *M. persicae* on rape (*Brassica napus*); the strain of virus Y was the one that has been used at our laboratory for aphid transmission studies during the past ten years; single adult apterae or late instar nymphs each probed once for less than a minute into an infected tobacco plant and then fed overnight on a young healthy tobacco plant (*Nicotiana tabacum* var. White Burley).

In another experiment, *M. certus* transmitted virus Y from potato to potato (*Solanum tuberosum* var. Green Mountain); nine out of 10 plants became infected when four aphids fed on each plant after first probing briefly into an infected plant.

On potato and tobacco *M. certus* behaved much the same as did *M. persicae;* both species usually probed the source plant for less than 30 seconds and both acquired virus Y in as little as 10 seconds, the briefest probes observed. Also, after being on the test plants overnight, most aphids had their stylets well inserted into the plants and had deposited numerous young. If on the basis of these few tests and observations we were to choose between these two species for ease of working with as vectors, it would be slightly in favour of *M. certus.*

In North America, the known hosts of *M. certus* are pansy and shepherd's purse (*Capsella bursa-pastoris*). Hille Ris Lambers (1946) concluded that *M. certus* is probably not important as a vector of viruses in horticultural crops in Europe, because it did not feed on potato, tulip, or sugar beet. But MacGillivray (1954) reported that the *M. certus* found in eastern Canada does feed on potato under glass, and we have confirmed this. It colonized the varieties Green Mountain, Katahdin, Bintze, Ostboote, and Hindenburg; but not Jubel or Eigenhemer. Furthermore it may be premature to conclude that an aphid does not spread viruses in crop plants because it does not feed on such plants and is normally not found colonizing them. Aphid vectors can acquire and transmit many viruses simply by probing briefly first into infected and then immediately into healthy plants. There is evidence that the spread of viruses in the field is mainly caused by winged aphids (Broadbent, 1959); and recent studies of aphid behaviour have shown that both on suitable and unsuitable host plants some alate

[1]Contribution No. 16, Research Station, Canada Department of Agriculture, Fredericton, New Brunswick.

forms of two species do in fact usually alight, probe, and depart without reproducing (Müller, 1958; Kennedy et al, 1959a, 1959b). Such behaviour would seem to be ideal for the spread of viruses transmitted during brief probes; and so long as such aphids do not reproduce, their importance as vectors might not be recognized.

After submitting this paper for publication, we read a recent article by Hille Ris Lambers (1959), in which he states: "MacGillivray's (1954) statement that she reared several generations (of *M. certus*) on excised potato leaves and young potato plants in 1953 seems doubtful in view of her remark that the aphid is very similar to *M. persicae;* in life the two species are extremely different. Her successful transmission results of 1952 were certainly the result of a mixed infestation, as our examination of her material showed." But Hille Ris Lambers did not quote MacGillivray's (1954) complete remark which was: "This aphid is very similar to *M. persicae* and cannot be separated from the latter species by the key of Mason (1940)." The remark referred to mounted specimens as seen under the microscope, just as one would suppose Hille Ris Lambers' (1959) remark: "However, for that purpose it was necessary that alate *Myzus certus* could be distinguished from the extremely alike alate *Myzus persicae* . . ." referred to specimens to be observed under the microscope or with a hand lens. MacGillivray (1954) clearly stated that in 1952 a mixture of *M. persicae* and *M. certus* occurred in her culture. Yet in 1953 and again in 1958 and 1959, the reddish aphids collected from *Viola tricolor* and reared on potato were *Myzus certus* only which, as pointed out by Hille Ris Lambers in his 1959 paper, are in life, very different from *M. persicae*. Specimens from the same culture as those used in our experiments were identified by MacGillivray as *Myzus certus* (Wlk.) only, and this identification was verified by Hille Ris Lambers in 1960. Since no one has been successful in Europe in rearing *M. certus* on potato and since we have reared it on several varieties of potatoes, possibly unknown differences exist between the European and North American forms of the species.

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Attractiveness of Different Foods and Flowers to the Adults of some Hymenopterous Parasites

By K. Leius

Entomology Research Institute for Biological Control, Research Branch
Canada Department of Agriculture, Belleville, Ontario

Many attempts to establish introduced parasites in Canada failed though the climatic conditions at their release points were apparently similar to those of their native habitats (Thorpe, 1930; Baird *et al.*, 1947). It is known that many adults of hymenopterous parasites feed on flowers, aphid honeydew, host body fluids, and other substances (Jackson, 1937; Thorpe and Caudle, 1938; Schneider, 1939; Györfi, 1945, 1951; Zoebelein, 1956). This brings up the possibility that nourishment from one or more of the above sources is necessary for survival and reproduction, and that some of the failures may have been because of the absence or scarcity of suitable adult food (Clausen, 1956). At present data on the food preferences of adult hymenopterous parasites are scarce. Except for a few field and laboratory observations, there are no experiments that demonstrate distinct preferences for one food over another. The results of the experiments described in the present paper demonstrate that adults of the species studied have preferences for some flowers and food substances tested.

Previous Work

According to Townes (1958), moisture is the dominant factor in the ecology of adult hymenopterous parasites. Dew may be important as a source of food because many wind-borne pollen grains of flowering plants are caught in dew on foliage. Adults caught in the morning often have their abdomens distended with water and pollen. Except on rainy days, however, such specimens are not found late in the afternoon.

The adults of some hymenopterous parasites visit flowering plants of many different families to obtain nectar and pollen. But a considerable number of the species with short mouth parts are restricted to the plants of one family (Györfi, 1945), particularly unbelliferous plants that have exposed nectaries. Clausen *et al.* (1927) reported that in Japan the native scoliid *Tiphia popilliavora* Roh. (Hymenoptera: Tiphiidae) fed solely on the blossoms of two umbelliferous plants, *Libanotis ugoensis* (Keidz.) Kitogava and *Patrinia scabiosaefolia* Fisch., and when imported into the United States it was found to feed exclusively on the flowers of wild carrot, *Daucus carota* L. Later, King and Holloway (1930) found that a satisfactory colonization point for *T. popilliavora* was one in which wild carrot was present in fair abundance. According to my observations and those of Muesebeck *et al.* (1951, p. 387), a number of meadow-inhabiting, late season species of ichneumonids, such as *Pristomerus olamonus* Vier. in Canada, can reach the nectaries of some tubular flowers, such as *Solidago* L. and *Aster* L. species, that are common in the autumn. Extrafloral nectaries, sometimes extremely minute, are important sources of food and moisture for many adults which may spend several hours a day working over the foliage of various plants (Clausen *et al.* 1927; Townes, 1958). The pollen of flowering plants is usually taken by the adults together with nectar and dew, but Györfi (1945) stated that *Ephialtes strobilellae* (L.) (Hymenoptera: Ichneumonidae) often ate the pollen of hazelnut, *Corylus avellana* L., an observation which could not be verified in the present experiments. The sap of plants was often mentioned in literature as a source of food for the adults. For example, Györfi (1945) reported that *Habrobracon vernalis* (Szépl.) (Hymenoptera: Braconidae) and *E. strobilellae* ate

softened pine resin. In the present experiments I repeatedly tried to feed *Scambus buolianae* (Htg.) and *Itoplectis conquisitor* (Say) adults on pine resin but without success, though they would try to eat it after they had been starved for several days. A seldom recognized source of food is provided by the "food hairs" on foliage and flowers of some plants (Kugler, 1955). My observations in the field and laboratory showed that *Giraudia plana* Prov. (Hymenoptera: Ichneumonidae) often bites such hairs. In the laboratory the adults remained alive on the leaves of the lesser burdock, *Arctium minus* (Hill) Bernh., for more than a month without any additional food except water.

Aphid honeydew is an important source of food and moisture, especially in early spring and late autumn when flowering plants are scarce. However, my field observations showed that on hot, sunny summer days the adults are absent from honeydew. Possibly their absence is connected with honeydew of low quality that results from early fermentation and quick drying in such weather. Györfi (1945) reported catching many species of ichneumonids, braconids, pteromalids, eulophids, and chalcids on honeydew, especially species that parasitize aphids, scale insects, and syrphid and coccinellid larvae. The host body fluid, or haemolymph, is a most important food for many, but not all, female adults of hymenopterous parasites. The males do not partake of this food and this suggests that this type of feeding is related to egg production. Predilection for host body fluids is exhibited only during oogenesis and maturation and even then the desire for additional carbohydrates occasionally may be dominant (Flanders, 1935). All efforts made in the present study to replace host body fluids as food with mammalian blood or liver failed.

Because of the difficulty of collecting and storing natural food for the laboratory maintenance of hymenopterous parasites, entomologists have been forced to use semi-natural, or even artificial, food that more or less resembled the natural food in content. Semi-natural foods, such as diluted or undiluted honey, sugar solutions, molasses, fruit marmalade, soaked raisins, and brewer's yeast, are well-known sources of carbohydrates, proteins of vegetable origin, and vitamins (Györfi, 1945; Trager, 1953). Host body fluids so necessary for egg development in the females of some hymenopterous parasites have been supplied by unnatural hosts like the wax moth, *Galleria mellonella* (L.), the flour moth, *Anagasta kuehniella* (Zell.), and other insect larvae and pupae that are available throughout the year (Trager, 1953). Györfi (1945), discussing the acceptability of these semi-natural foods, observed that ichneumonids and some braconids were more often attracted to sugar solution than to diluted honey. On the other hand most of the chalcids, pteromolids, torymids, and some braconids preferred diluted honey to sugar solution.

In the field adults of hymenopterous parasites find a rich supply of different food that varies greatly in content, not only between sources but also within the same source (Kugler, 1955). Most insects undoubtedly have well-developed senses that permit them to find and accept appropriate food. These senses probably also enable them to reject some potentially harmful substances. But acceptance or rejection of a nutrient material is not in itself a certain indication of its fundamental nutritional value to the insect concerned (Trager, 1953). According to Kugler (1955), adults are usually guided to the vicinity of their natural foods by the visual senses, and when an insect in flight enters an area of odour stimulation it will land if attracted but will continue flight if not. When attracted by odour the insect will taste the food and if it is acceptable feeding will follow.

Materials and Methods

Adults of *I. conquisitor*, *S. buolianae* and *Orgilus obscurator* Nees were selected for the study of their food preferences and the attractiveness of different flowers. The adults that emerged on the same day from the population reared in the laboratory were kept in a large cage, fed on sugar solution, provided with their hosts, and used for experiments after four hours starvation and when all females were ready to oviposit. Experiments were conducted in standard cages (15″ x 8-¾″ x 8-¾″) each containing both females and males. In experiments with *I. conquisitor* the following foods were tested: 37.5 per cent sucrose solution, Scots pine pollen (one per cent pollen grains in suspension) in 37.5 per cent sucrose solution, diluted honey with 37.5 per cent sugar content, soaked raisins, wax moth pupae, and honeydew exuded by the aphid *Myzocallis alhambra* Davids. on leaves of burr oak, *Quercus macrocarpa* Michx. In experiments with *S. buolianae* the same foods were used except soaked raisins, but wax moth larvae were used instead of pupae. Distilled water was used to dilute foods and for drinking purposes. The liquid foods were provided on ¾ inch lengths of dental cotton. All foods were placed in a row near the rear of each cage and their position systematically changed on consecutive days. In studies of the attractiveness of flowers, freshly cut bouquets of more or less equal size of each species were placed in jars of water in a row near the rear of each test cage and their position systematically changed on consecutive days. Flowers of the following species were selected for testing the preferences of *S. buolianae* and *I. conquisitor*: wild mustard, *Sinapis arvensis* L., white sweetclover, *Melilotus alba* Desr., wild parsnip, *Pastinaca sativa* L., silky milkweed, *Asclepias syriaca* L., and annual sowthistle, *Sonchus oleraceus* L. In the experiment with *O. obscurator* the three umbelliferous plants, water hemlock, *Cicuta maculata* L., wild parsnip, *P. sativa* (L.), and wild carrot, *D. carota*, were tested after preliminary experiments with various other plants showed that only Umbelliferae were attractive.

After an adult flew to one of the foods or flowers and began to feed it was removed from the test cage, recorded, and kept in a separate cage. The duration of each day's test was either four hours or until all insects had responded, whichever was shorter. At the end of four hours any adults left in the test cages were recorded as not having responded and observations on them were discontinued. All adults were returned to their cages, provided with sugar solution and hosts during the night, and used the following afternoon, after four hours of starvation, for another test. Each group of insects in any one test cage were used on 15 or 20 consecutive days, and two or three test cages were operated simultaneously on each day. The room in which these experiments were made had a constant temperature of 76°F. (±1) and a constant relative humidity of 66 per cent (±1).

Results

Experiments with Itoplectis conquisitor (Say)

I. conquisitor is a native internal parasite of many lepidopterous pupae in North America. Among the pests of economic importance that it attacks are: *Pieris rapae* L., *Porthetria dispar* L., *Malacosoma americanum* (F.), *M. disstria* Hon., *Ostrinia nubilalis* (Hon.), *Rhyacionia buoliana* Schiff., *Carpocapsa pomonella* L., and *Choristoneura fumiferana* Clem. (Muesebeck *et al.*, 1951). Such a wide variety of potential hosts enables the females of this species to feed in the field or laboratory on host body fluids of a variety of species (Johnston, 1913). But the diet of this species is not limited to pupal body fluids, at least in the

laboratory, because diluted honey, sucrose solution, and soaked raisins were often eaten by both females and males as substitutes for nectar and other natural foods (Thorpe and Caudle, 1938; Arthur, 1956). There are no records in the literature on the natural food of adults of *I. conquisitor*.

In the present study, when flowering plants are scarce in spring and autumn numerous females and males of *I. conquisitor* were found feeding on the honeydew exuded by the aphid *Schizolachnus pini-radiatae* (Davids.) on the needles of red pine, *Pinus resinosa* Ait.

Females were often observed in the field feeding on the body fluids of pupae of *P. rapae* and *R. buoliana* and in the laboratory body fluids were obtained from wax moth pupae.

Attractiveness of Different Foods to Adults of I. conquisitor

In the experiment with females, tests were conducted on 20 days with 25 insects in each of two cages; the experiment with males comprised tests on 15 days with 15 insects in each of two cages.

Experiment with Females.—At the beginning of the preoviposition period the females fed only on carbohydrate foods. During this time, which lasted three to four days, the females paid no apparent attention to the wax moth pupae. The desire for host body fluid was observed one or two days before oviposition when females often punctured the pupae and ingested the droplets of body fluid that exuded. Host feeding was not continuous as the females required carbohydrates and vegetable proteins to prolong life. When all females were ready to oviposit, each run of experiments was carried out only after the insects were starved four hours. This experiment showed (Fig. 1-B) that all foods were attractive to a certain degree, and that diluted honey and pollen in sucrose solution were the most attractive among the carbohydrate foods tested whereas sucrose solution was the least attractive.

Experiment with Males.—Selection of food by the males was different from that by the females and apparent preferences for one diet over another were much more distinct (Fig. 1-C). Of the foods investigated, pollen in sucrose solution attracted more males than did the other foods. Honeydew on burr oak leaves and soaked raisins were the least preferred. The males were not attracted to the wax moth pupae because they do not ingest the host body fluids.

Attractiveness of Different Flowers to Females of I. conquisitor

Observations in the field showed that *I. conquisitor* visited a great number of flowering plants of a number of families. It was captured on: bladder campion, *Silene cucubalus* Wibel; yellow sweetclover, *Melilotus officinalis* (L.) Lam.; white sweetclover, *M. alba* Desr.; alfalfa, *Medicago sativa* L.; wild parsnip; *P. sativa;* wild carrot, *D. carota;* silky milkweed, *A. syriaca* and field bindweed, *Convolvulus arvensis* L. It was found that adults, especially males, appeared to prefer umbelliferous plants to other flowering plants.

Tests were made on 15 days with 15 females in each of three cages. This experiment (Fig. 1-A) showed that wild parsnip, an umbelliferous plant, attracted most of the females tested. Silky milkweed, white sweetclover, and wild mustard were next in attractiveness. The annual sowthistle had relatively little, if any, attractiveness in the presence of the other flowers.

Experiments with Scambus buolianae (Htg.)

S. buolianae is a recently (1956) introduced external larval parasite of the pine shoot moth, *R. buoliana*, and is not yet known to be established in Canada.

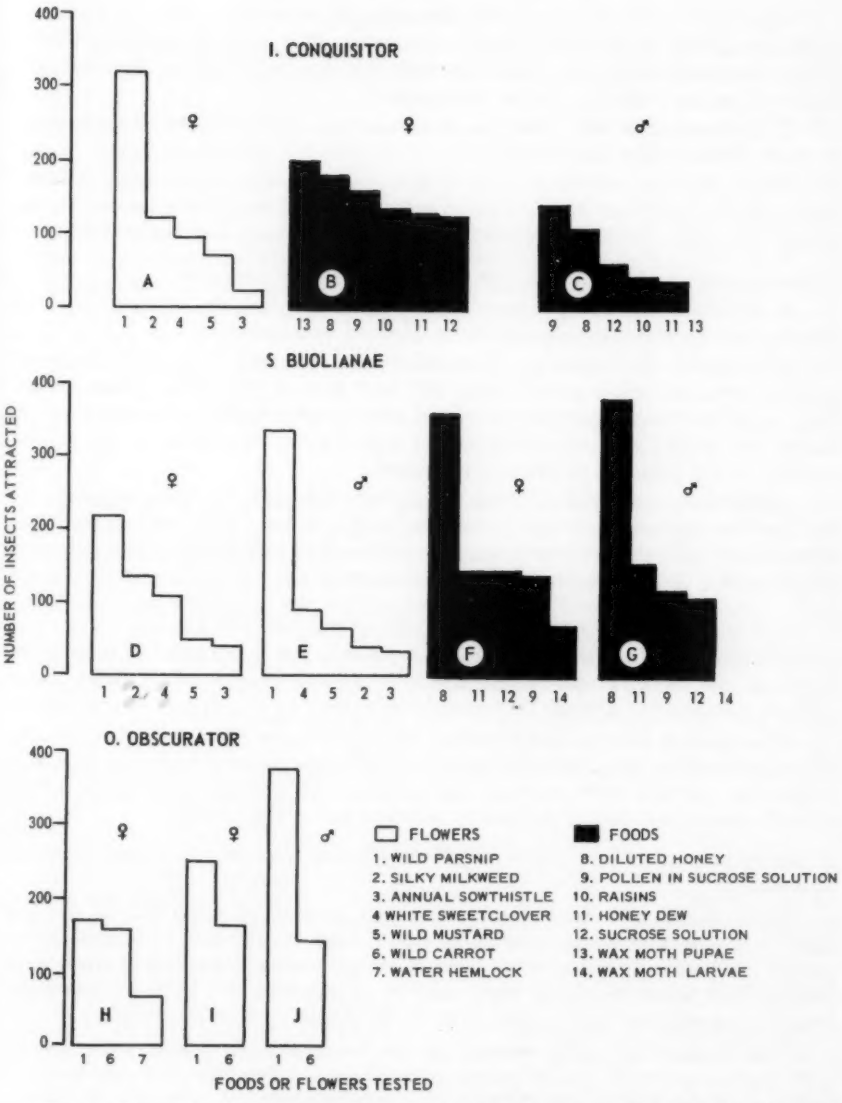

Fig. 1. Histogram showing attractiveness of various flowers and foods to the adults of *I. conquisitor*, *S. buolianae* and *O. obscurator*.

Attractiveness of Different Diets to Adults of S. buolianae

The preoviposition period of *S. buolianae* was from six to nine days in the laboratory. Females usually did not feed on the day on which they emerged. On the second day they fed on carbohydrate diets for from two to six days but did not touch wax moth larvae. After this period the females started to feed on host body fluids in addition to the carbohydrate diets and this type of feeding normally continued until death.

Experiment with Females.—Three test cages were used, with 20 insects in each, and tests were run for 15 days. The results (Fig. 1-F) showed that diluted honey attracted about three times as many females as the sucrose solution, the pollen in sucrose solution, or the honeydew.

Experiment with Males.—In this experiment tests were conducted on 20 males in each of three cages for 15 days.

The results showed (Fig. 1-G) that more males were attracted to diluted honey than to any one of the other foods. As usual, wax moth larvae did not attract the males, probably because they do not feed on host body fluids.

Attractiveness of Different Flowers to the Adults of S. buolianae

In this laboratory experiment tests were conducted on 15 days with 20 females and 20 males simultaneously in each of two cages.

Experiment with Females.—This experiment indicated (Fig. 1-D) that wild parsnip attracted more insects than did any one of the other plants tested. Silky milkweed was apparently preferred next to wild parsnip and white sweetclover was third. Annual sowthistle and wild mustard had little, if any, attractiveness in the presence of the other flowers.

Experiment with Males.—Wild parsnip was the only flowering plant in the test that was distinctly attractive to the males (Fig. 1-E). Silky milkweed, white sweetclover, wild mustard, and annual sowthistle had individually relatively little attractiveness in the presence of the wild parsnip.

Experiments with Orgilus obscurator Nees

O. obscurator is an internal hymenopterous, larval parasite of pine shoot moth, *R. buoliana.* It was unintentionally introduced into the United States with its host in 1931, though discovered there prior to this date (Clausen, 1956).

Observations on the feeding habits of adults in the laboratory showed that males and females restricted their diet to carbohydrates and proteins of vegetable origin and did not feed on host body fluids. They were often attracted to diluted honey, and seldom to sucrose solution and soaked raisins.

Attractiveness of Three Different Umbelliferous Flowers to Females of O. obscurator

Early attempts to feed adults on various flowers of a number of families failed. It was found later that they would feed on flowers of umbelliferous plants. Accordingly three very common umbelliferous plants, wild carrot, wild parsnip, and water hemlock, were used in an experiment. In this experiment tests were conducted on 15 days, with 15 females in each of two cages.

The results (Fig. 1-H) showed that in most cases the insects went first to wild parsnip and wild carrot in approximately equal numbers, and that only 17 per cent of the first visitations were to water hemlock.

Attractiveness of Wild Parsnip and Wild Carrot to Adults of O. obscurator

The absence of males in the previous experiment and the lack of preference between wild parsnip and wild carrot in the presence of water hemlock promoted further experiments using only wild parsnip and wild carrot. In this experiment tests were made on 15 days with 15 females in each of two cages; the experiment with males comprised tests on 20 days with 15 insects in each of two cages. The results (Fig. 1-I, J) showed that when only these two plants were present there were many more instances of attraction to wild parsnip than to wild carrot.

Discussion

Though the experiments and observations described here are limited, they indicate that the feeding habits of the adults differ greatly between the species studied. *Itoplectis conquisitor* and *Scambus buolianae* are attracted to host body fluids but *Orgilus obscurator* does not feed on these. *I. conquisitor* and *S. buolianae*, though preferring umbelliferous flowers, were attracted to some extent to other flowers. *I. conquisitor* and *S. buolianae* were also attracted to a variety of semi-natural foods but preferred diluted honey. On the other hand the adults of *O. obscurator* were attracted only to umbelliferous flowers. Such differences in the acceptance or rejection of food sources are important factors in the establishment of imported parasites. When certain food sources are absent or their distribution is limited the adult parasites may not be able to find adequate food supply for their survival. This conclusion is consistent with the results of Gardner (1938), who studied the influence of feeding on *Tiphia vernalis* Roh. (Hymenoptera: Tiphiidae), and with King and Holloway (1930), who successfully colonized *Tiphia popilliavora* in the United States.

Summary

Studies were made on the food preferences of three hymenopterous parasites: *Itoplactis conquisitor; Scambus buolianae;* and *Orgilus obscurator*. Each species showed an order of preference for various natural and semi-natural foods. Females of *I. conquisitor* and *S. buolianae* fed on host body fluids whereas those of *O. obscurator* did not, nor did the males of any of these three species. Both sexes of *O. obscurator* were attracted only to umbelliferous flowers, and preferred wild parsnip. The other two species were also most attracted by umbelliferous flowers but were attracted to flowers of other families as well.

These preliminary studies indicate that information on adult feeding habits is essential when parasites are being introduced for biological control purposes. If a favorite food, such as umbelliferous flowers, is absent from the release area the parasites have less chance to become established.

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The Bionomics of *Profenusa thomsoni* (Konow) (Hymenoptera: Tenthredinidae) a Leaf-Mining Sawfly on *Betula* spp.[1]

By J. Lynton Martin
Forest Insect Laboratory, Sault Ste. Marie, Ontario

Infestations of *Profenusa thomsoni* (Konow) have occurred throughout most of northeastern, central, and southern Ontario since 1948 (Sippell, MacDonald, and Wallace, 1956), but before 1955 (Lindquist, 1955), its presence was not recognized because it was confused with the common birch leaf miner, *Fenusa pusilla* (Lep.).

An investigation of the biology of *P. thomsoni* was begun in 1956 and continued through 1957. This paper describes the life history and general ecology of the insect as it occurs in the area immediately north of Sault Ste. Marie, Ontario, on the eastern shore of Lake Superior. Descriptions of larval morphology, made with material provided by this study, have been published (Watson, 1959).

Systematic Position, Distribution, and Hosts

According to Benson (1959), this species was originally described from European material as *Fenusa thomsoni* Konow (1886). Benson reorganized the genera of the tribe Fenusini in 1941, and called the species *Profenusa thomsoni* (Konow) (Benson, 1941). Benson considers MacGillivray's *Messa alumna* (MacGillivray, 1923) and Ross' *Profenusa alumna* (Ross, 1951) synonymous (Benson, 1959).

The insect is known to occur in Europe and Japan (Benson, 1959), and in North America it has been collected in Illinois, Massachusetts, New Hampshire, New York, (Ross, 1936), Wisconsin (Benson, 1959), Manitoba[2], New Brunswick[3], and Ontario. Its hosts in North America are *Betula papyrifera* Marsh., *B. lutea* Michx., and *B. populifolia* Marsh. Benson states that the species is now holarctic in distribution, and suggests that it may have been introduced into North America (Benson, 1959).

[1]Contribution No. 606, Forest Biology Division, Department of Agriculture, Ottawa, Canada.
[2]Personal communication from the late R. Lambert, Systematic Entomology and Biological Control Unit, Department of Agriculture, Ottawa.
[3]Personal communication from D. C. Eidt, Forest Biology Laboratory, Fredericton, New Brunswick.

Life History

Emergence of adults from hibernation

In 1957, adults were first seen on July 16, and scattered individuals were still present on August 9. Although several thousand specimens were examined, no males were found. The females emerged from the soil during the warmer part of the day, rested on the leaves of the ground cover for a short time, and then flew upward to the birch leaves.

Emergence appeared to be controlled to a great extent by temperature, and this resulted in considerable variation in the number of specimens present on trees at different times during the flight period. For example, two or three days with temperatures reaching 70° F. or higher, and night-time temperatures of not below 50° F., resulted in the appearance of large numbers of adults. If the temperatures dropped below this range, emergence fell off markedly.

Oviposition

The eggs are laid singly between the upper epidermis and the palisade layer of the birch leaf (Fig. 1, B). They are placed beside a vein, and are usually concentrated in the central body of the leaf, with few if any near the leaf margins (Fig. 1, A). The time required to lay one egg varies from 17 to 94 seconds.

The sucker growth, up to about four feet in height, growing in partial shade in a protected or semi-protected position, is preferred for oviposition, but this preference is obvious only when the adults are not abundant. When crowding occurs, eggs are laid on birch leaves in practically every type of habitat, and at heights of over 35 feet but the young, growing leaves at the tips of the stems are never utilized.

These insects are extremely sensitive to changes in temperature and humidity. A few adults begin to lay eggs when the temperature reaches 60° F., but most of them remain inactive until the temperature rises above 65° F., and peak activity is only attained above 70° F. Oviposition never begins before the dew has dried off the leaves in the morning, and ends before dew-point in the evening. All activity ceases with the appearance of rain. The adults spend the late afternoon, night, and early morning on the undersides of the leaves; at those times they are quite torpid and can be collected with ease.

Several examples from daily field records illustrate the sensitivity of this species: on July 24, the morning was clear with no wind, and by noon the temperature had reached 69 ° F., and the adults were quite active. By 2.15 p.m., the sky was overcast, the temperature was still 69° F., but the relative humidity had risen to 74%, and all the adults had moved to resting places under the leaves. At 2.30 p.m., rain began to fall and there was no further activity that day. On July 30, the temperature reached 68° F., but a light breeze carried a fog in over the land preventing any adult activity.

The records for July 29 show a typical, fine day behaviour pattern:

9.30 a.m. – Temperature 66° F., Relative Humidity 80%, clear, light breeze. No activity, adults on undersides of leaves.

11.00 a.m. – Temperature 70° F., Relative Humidity 70%, high adult activity.

1.45 p.m. – Temperature 72° F., Relative Humidity 66%, intense activity, as many as seven adults ovipositing on the same leaf at a time.

4.30 p.m. – Temperature 68° F., Relative Humidity 84%, little activity, many adults on undersides of leaves.

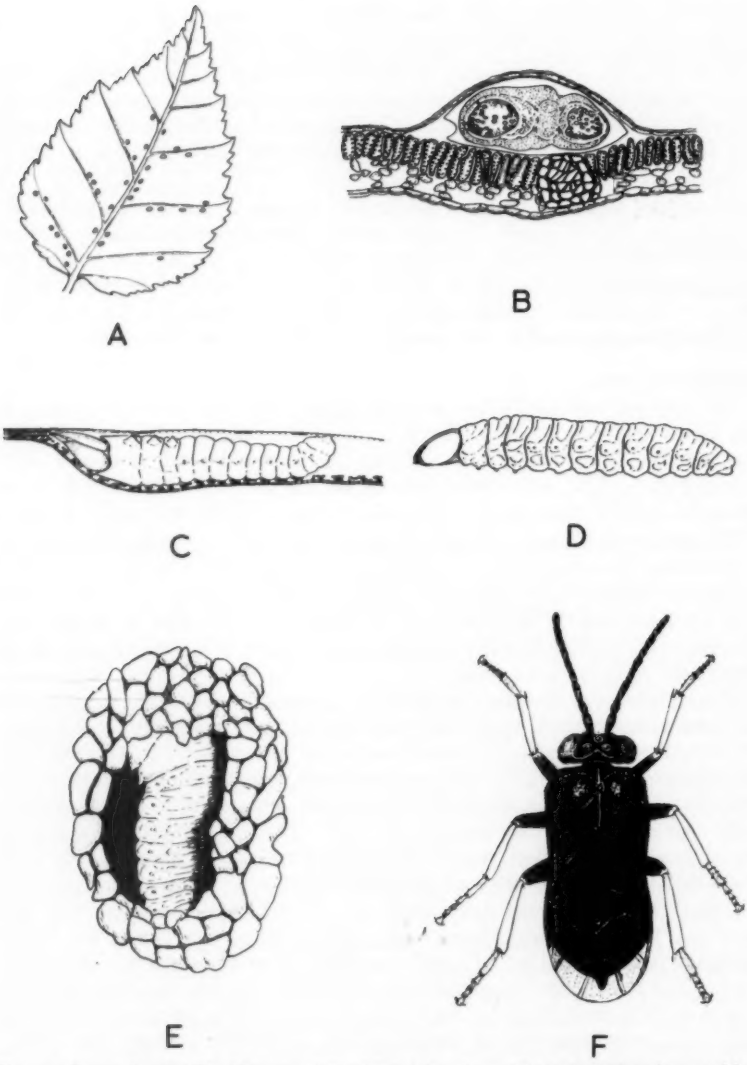

Fig. 1. Stages in the life history of *P. thomsoni*. A — Birch leaf showing position of eggs. B — Vertical section of leaf showing egg. C — Vertical section of leaf-mine showing feeding position of larva. D — The sixth-instar larva. E — The pupal case with side opened to show prepupa. F — The adult.

A combination of the effects of temperature and humidity exerts a strong controlling influence on the actions of the adults during oviposition. Temperatures above 70° F. encourage high activity only if the humidity remains at or below 70%.

The effects of adult numbers on oviposition behaviour were clearly marked, and were divided into three phases. In the initial phase, adults were few in numbers and most leaves were free of eggs. The females crawled rapidly over

the leaves, paused here and there, and only deposited eggs after a careful inspection. During one visit, a single female laid from one to five eggs per leaf, but the same females often returned to the same leaves a few minutes later and repeated the procedure.

The second phase occurred when adults were more numerous and most leaves already bore a few eggs. The females acted in an extremely nervous manner, inspected one leaf after another, often remained on one leaf for three minutes or more and then left without depositing any eggs. During this phase, many adults moved away from the sucker growth and lower branches into the upper parts of the trees.

The third phase occurred when adult numbers were extremely high, with as many as seven females ovipositing on a single leaf at the same time. The adults laid their eggs rapidly with little or no inspection of the leaf beforehand. Before this phase, many leaves contained as many as 30 eggs each, but after this phase the number was often doubled; some of the larger leaves on the sucker growth contained nearly 300 eggs.

The Egg

The eggs appear as small, elliptical blisters on the upper surface of the leaf. Typical of many sawfly eggs, they swell after insertion into the leaf tissue, and in doing so they lift the epidermal cells of the leaf. These lifted cells appear as a whitish ring around the egg. At this stage, the egg is translucent and measures 0.5 mm. in width. As the embryo develops, the egg turns brown, and the fully developed larva is easily seen curled within the egg two days before hatching. The eggs hatch in about 12 days.

The Larval Period

The larval period consists of five feeding instars and one prepupal instar. The feeding instars are similar in that the mouthparts are directed forwards in the same plane as the body, but there is a gradual change from a flattened body in the first instar to a cylindrical body in the fifth.

The newly-hatched larva is about 1 mm. in length, and has a comparatively large, triangular, tan-coloured head; flattened dorsoventrally, prognathous and heavily sclerotized. The prothorax is wider than the head, and bears a large central and two lateral dark brown markings on the ventral surface. The body tapers rapidly from the prothorax to the tip of the abdomen, and is translucent white with the green colour of the digestive tract obvious.

The fifth, or final feeding instar, reaches 7 mm. in length. The head is similar to that of the earlier instars. The thorax is more heavily sclerotized, and bears small oval brown markings on the ventral side of the meso- and metathorax. The thoracic legs and the abdominal spiracles are brown and prominent. The body is cylindrical, and is dull, translucent white with a pebbled surface. (For more detailed larval descriptions, see Watson, 1959).

The period of each stadium increases from 4 days in the first to 6½ days in the fifth instar. These periods vary somewhat depending upon the number of larvae in the leaf, but the average periods recorded in the field under uncrowded conditions were as follows: first instar, 4 days; second instar, 4 days; third instar, 4½ days; fourth instar, 5 days, and fifth instar, 6½ days.

As stated above, the eggs are deposited beside a leaf vein, and when the larva hatches it invariably leaves the egg from the side opposite the vein. The first-instar mine is narrow, and with its single line of frass pellets, looks almost serpentine. During the second instar it assumes a typical blotch shape and the frass is

dropped at random. The mine is seen as a light-brown, irregularly-shaped, slightly-raised area on the upper surface of the leaf, but it is not readily distinguished from the underside.

The fully developed embryo lies on its back within the egg, and the larvae remain in this position throughout their lifetime in the leaf. They restrict their feeding entirely to the palisade layer, and Fig. 1, C shows how the inverted position and the head structure are suited to this type of feeding. During the first two instars, the body of the larva lies perfectly flat in the mine, but in the last three instars, the tip of the abdomen curves upward and rests against the upper epidermis of the leaf (Fig. 1, C). The third-, fourth-, and fifth-instar larvae use the tip of the abdomen in a pushing manner to help them in their movements in the mine. Upon reaching the sixth instar, the larva cuts a small, circular hole in the upper surface of the mine, crawls out, and drops to the ground.

One larva requires about 5.3 sq. cm. of leaf tissue to reach the sixth instar. Thus, the average birch leaf provides sufficient food for approximately five or six larvae, with the smaller, upper leaves of large trees supporting about two, and the large leaves of the sucker growth about eight larvae.

In all but very light infestations, the number of larvae per leaf exceeds the maximum number for which the leaf can provide sufficient food. The mines usually coalesce, and as many as 40 larvae are commonly found in one mine. The larvae do not have any cannibalistic tendencies, and a dozen or more larvae may often be seen feeding quietly in a tightly packed row. When the palisade cells have been completely consumed, all the larvae, regardless of stage of deevlopment, drop to the ground. Those which have reached the latter part of the fifth instar, moult into the sixth instar after leaving the mine but the rest die.

The sixth-instar larva is smaller than the fifth, reaching a length of only 6 mm., and although it is translucent white immediately after moulting, it changes rapidly to a deep yellow. Unlike the earlier instars, this stage has a hypognathous head, and crawls in the typical sawfly manner, rather than by the squirming, pushing method of the feeding instars.

The larvae are feeble burrowers and will usually spend considerable time searching for a passageway into the soil. On sifted soil or pure sand, only a few individuals are able to leave the surface, but when openings are made with a needle, the larvae enter the soil readily. Under field conditions, they seek natural openings and the depth to which they penetrate seems to depend largely on the ease of movement.

Pupal cells are found at depths of one to four inches beneath the soil surface, often at the lower margin of the humus layer but seldom in the mineral soil. To construct the pupal cell, the larva merely squirms around at the end of its tunnel and smears a yellow, mucilaginous secretion over the soil particles. This material cements the soil particles together, and hardens to form a smooth, shining, brown lining (Fig. 1, E).

About two days are required for the larva to enter the soil and complete its pupal cell. After this time, the larva shrinks to half its original length, the head bends sharply in a ventral-posterior direction, and the prepupa remains inactive throughout the winter. In 1957, the larvae began entering the soil about the middle of August and continued to drop from the leaves until mid-October.

The Pupa

Pupation occurs early in July and the stage lasts for about eight days. The newly-formed pupa is approximately 4 mm. long, the compound eyes are reddish brown, the head, antennae, legs, wings and ovipositor are translucent white, and

the thorax and abdomen are pale yellow. As development proceeds, the whole body changes to a bluish grey and finally to black.

The Adult

MacGillivray (1923) described the adult and Ross (1936) illustrated the male and female genitalia. Although no males were encountered during this study, Ross (1936) considers MacGillivray's *Messa appota* male (MacGillivray, 1923) to be synonymous with *P. thomsoni*, and it is possible that males do occur at times.

The white tibiae and tarsi (Fig. 1, F) are useful characters in distinguishing this species from other leaf-mining sawflies found on birch.

Insect-Host Relationships

As stated above, observations made during the early part of the flight period, when adults were not too numerous, indicate that the preferred habitat of *P. thomsoni* is the semi-protected, partially-shaded conditions of the closed stand in which may be found large birch trees, up to and above 35 feet in height, with an abundance of sucker growth. However, with the appearance of large numbers of adults, oviposition takes place on birch trees of all ages growing in almost every type of situation.

The distribution of infested trees throughout the stands examined was erratic and without pattern. In some cases every birch tree in a stand bore a heavy larval population, whereas in other cases only scattered trees were affected. Such factors as shade, exposure, and aspect apparently had little effect on the density of the populations in heavily infested areas, with numbers as high in the closed forest as on the open lakeshore.

The distribution of feeding larvae on the trees was established as follows: Three branches were clipped from each five-foot height interval, 100 leaves were picked from each branch, and the 300 leaves were mixed in a paper bag. One hundred leaves were then withdrawn from the bag and the number of larvae per leaf recorded. Since observation indicated no significant difference in size of population on the north, south, east, or west sides of the trees, the compass points were disregarded during sampling.

Two groups of trees were sampled: the first were heavily infested bearing an average of six larvae per leaf, and the second were lightly infested with an average of two larvae per leaf. Fig. 2 shows that the largest numbers of larvae in both heavy and light infestations were concentrated in the foliage below 10 feet, with smaller numbers of larvae from there to the tops of the trees.

Since larval feeding takes place late in the season after the trees have completed most of their year's growth, the effect of this insect on the trees is probably negligible. In heavily infested stands, a premature leaf drop occurs, but this takes place only about two weeks before the usual fall, and is probably of little consequence to the overall health of the trees.

The reports of the Forest Biology rangers, Forest Insect Laboratory, Sault Ste. Marie, for the period 1951 to 1957 provide some information regarding the duration of infestation in particular stands. These reports indicate a population buildup over a three-year period, maintenance of extremely high numbers up to five years, and a decline in two or three years.

Mortality Factors

Adult

The adults of *P. thomsoni* experienced heavy predation by ants and spiders. When the sawflies emerged from the soil in mid-summer, they rested for about

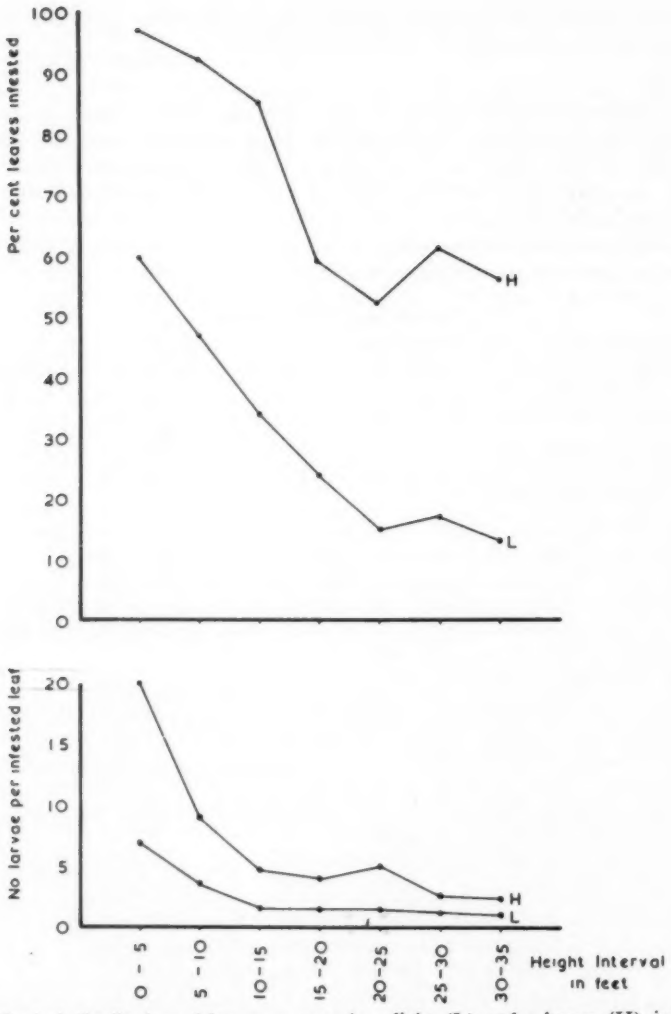

Fig. 2. Vertical distribution of larvae on trees in a light (L) and a heavy (H) infestation.

an hour on the leaves of the ground-cover plants, probably to allow their wings to mature, and during this period the predators took a heavy toll.

Predation continued throughout the flight period, with many females being captured during the act of oviposition. Both web-spinning and hunting spiders were present, but the hunters were the most effective predators. Although several species of ants were common, only one species, *Formica fusca* L., was seen feeding upon the sawflies.

Egg

Undermining by feeding larvae was the most important factor in egg mortality. The eggs seemed dependent upon the leaf tissue to a considerable extent, possibly for the maintenance of their water balance, and when the tissue beneath

the eggs was eaten by larvae, the eggs failed to hatch. Observations showed that the extent of egg mortality varied considerably, but it often reached 80 per cent, with an average value of about 50 per cent per leaf.

The degree of egg mortality due to undermining depends upon the length of the period during which the eggs were laid, and not upon the number of eggs per leaf. For example, if 50 eggs were laid on a leaf in one day, they will all have a good chance of hatching, but if 50 eggs are laid on a leaf over a period of two weeks, the eggs laid during the last week will have little chance to complete their development before they are undermined by the earlier-hatched larvae.

The successive waves of adults ovipositing on the same foliage, as described above, are the basic cause of the high egg mortality. In heavy infestations, only a small percentage of the eggs laid after the first two weeks of the flight period on leaves below 10 feet in height are able to hatch.

Larva

The most important larval mortality factor was undoubtedly starvation in all but very light infestations. When a birch leaf was completely mined, the larvae, regardless of their stage of development, dropped to the ground. Here they were unable to enter other leaves, and only those which had reached the latter part of the fifth instar could moult into the sixth instar and enter the ground to pupate. The remainder died of starvation or were eaten by predators.

It was shown above that the average birch leaf provided sufficient food for about five or six larvae to reach the sixth instar. Medium- to heavily-infested foliage contained as many as 40 larvae per leaf, particularly below 10 feet in height. Larval mortality usually approached 100 per cent in leaves containing 10 or more larvae. It was interesting to note that in medium and heavy infestations, although the adults persisted in favouring the lower foliage levels for oviposition, the bulk of the surviving popualtion came from the less crowded upper portions of the trees.

The second most important factor operating in the natural control of this species during the larval stage was predation. When the sixth-instar larvae dropped to the ground, they spent considerable time searching for a natural passageway into the soil. During this period, they were heavily preyed upon by the ant *F. fusca*, and probably by other insects and spiders.

After the larvae entered the soil and constructed their pupal cells, wireworms were observed preying upon them. No quantitative statement regarding predation can be made here, but such a figure would undoubtedly be extremely high. In some locations where hundreds of larvae reached the soil, careful sieving a week or two later yielded only a very few scattered pupal cells.

Although hymenopterous parasites were seen depositing their eggs on larvae during late July and throughout much of August, larval mortality due to parasitism during the mining period was virtually non-existent but an examination of pupal cells in the fall showed that 22 per cent of the prepupae died because of parasites.

Lathrolestes sp., an ichneumonid species, was reared.

Pupa

No records of pupal mortality are available.

Summary

P. thomsoni is a leaf-mining sawfly infesting white, yellow, and wire birch in the northeastern United States and in Canada from New Brunswick to Manitoba

The adults emerge in mid-July and deposit their eggs in the upper sides of the leaves. There are six larval instars, the first five feed in the leaf, and the sixth enters the ground and overwinters as a prepupa. Pupation takes place in early summer in an earthen cell several inches beneath the soil surface.

Although preference is shown for leaves less than 10 feet from the ground in semi-protected, partially-shaded situations, both large and small birch trees in almost every type of habitat will be attacked during heavy infestations. The lateness of the larval feeding probably results in little or no appreciable injury to the trees.

Adults and larvae experienced heavy predation by ants and spiders. In heavy infestations, egg mortality was extremely high due to larval undermining, and larval mortality was very heavy due to starvation. The prepupal instar suffered about 22 per cent mortality from hymenopterous parasites.

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Spruce Budworm Parasite Investigations in the Lower St. Lawrence and Gaspé Regions of Quebec[1]

By J. R. Blais
Forest Biology Laboratory, Quebec

Introduction

A spruce budworm outbreak started in Quebec and adjoining parts of New Brunswick in 1949 and spread each year until by 1955 most balsam fir stands within an area of 32,000 square miles were attacked. Approximately 45 per cent of this area was in the Lower St. Lawrence and Gaspe regions of Quebec. In Quebec, important population reductions took place in various sectors of the outbreak area as a result of unfavourable weather conditions in 1956 and 1957 (Blais, 1958a, 1958b), and the final collapse occurred in 1958 when populations returned to the endemic level throughout the area (Blais and Martineau, 1958). In New Brunswick, a relatively small outbreak area remained at the end of the summer in 1958 (Webb *et al.*, 1959). The large-scale aerial applications of DDT begun in New Brunswick in 1952, and in Quebec in 1954, were continued until 1958. Biological studies in connection with the spraying were carried out in both provinces. In Quebec these studies consisted of assessing spruce budworm

[1]Contribution No. 581, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

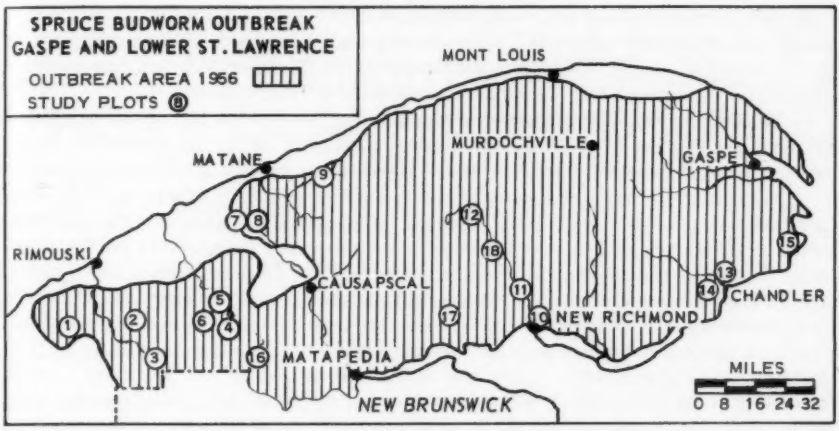

Fig. 1

population fluctuations in both sprayed and unsprayed areas and in determining, where possible, the causes for these fluctuations. All factors associated with changes in population could not be adequately measured over such a large territory, but a real attempt was made to obtain information on parasitism. The present paper deals with this aspect of the studies.

Investigations on the parasite complex of the spruce budworm in the Lower St. Lawrence and Gaspe Peninsula were begun in 1954 under the direction of L. Daviault, and were continued during 1955-58 by the writer. Information on the parasite complex was obtained from as many localities as possible, to provide an appraisal of conditions throughout the general area. In addition to recording annual fluctuations of individual parasite species, an effort was made to evaluate increases or decreases in total parasitism in relation to changes in populations of the spruce budworm.

Methods

Collections of spruce budworms were made from 18 plots established in mature balsam fir stands (Fig. 1). However, no more than 11 plots were used in any one year; some of the plots had to be abandoned for various reasons and new plots were established periodically. The years in which the experimental plots were used are shown in Table XII. Previous knowledge of parasite behaviour prompted the collection of material at the following times: the peak of the fourth instar, the peak of the sixth instar, and the peak of the pupal stage. All known parasites of the spruce budworm in Eastern Canada, with the exception of egg parasites, are recovered by this schedule (McGugan and Blais, 1959).

Collections were made by taking mid-crown branches from balsam fir trees with pole pruners. Usually 200 to 400 insects were obtained from each plot for each collection. When population levels were very low, as in recently sprayed plots or in the last year of the outbreak, a smaller sample was obtained. At the time of each collection the population level was established from counts of living budworms on one 18-inch branch-tip from the mid-crown of each of ten co-dominant balsam fir trees; the same trees were sampled throughout the season.

All larvae and pupae were kept under observation in eight-ounce screw-topped jars. Larvae were provided with fresh food every third day, and were transferred to separate jars after pupation. Parasite cocoons, puparia, and adults were removed when observed. The cocoons and puparia were placed in glass

vials for further rearing and were examined every day. All adult parasites that could not be readily identified were pinned and submitted for identification to J. P. Laplante of the Quebec Laboratory or to members of the Entomology Research Institute of the Canadian Department of Agriculture.

In addition to determining the incidence of parasitism by *Apanteles fumiferanae* and *Glypta fumiferanae* by rearing, a number of spruce budworm larvae obtained in 1955 and 1957 were dissected prior to the emergence of these parasites.

While certain parasite species affected the host during the same period, other parasites or groups of parasites affected other periods. Because the parasites acted in sequence, calculations for all per cent mortality values given in this paper were based on the method originally advocated by Howard and Fiske (1911). All mortality factors acting on the host population are not known, and therefore *real mortality* through parasitism cannot be determined. However, mortality from parasitism is known and an approximation of the total mortality by this factor can be calculated. Since the sequential action of the parasites is considered in these calculations, the percentage mortality caused by the late-emerging parasites is less than would be the *apparent mortality*. A new term must be given to this percentage mortality to distinguish it from *real mortality* which refers to the percentage of the original population that died, and *apparent mortality* which is the proportion of the population killed at the time of emergence of a given parasite species. For the lack of a better term, and because this percentage mortality has a relative rather than an absolute value, it will be called *relative mortality*. In effect, *relative mortality* as calculated here is the same as would be *real mortality* should entomophagous parasites be the sole cause of mortality in the host population. Since *relative mortality* is based solely on mortality occasioned by parasites in this study, the term *relative parasitism* can be applied as a synonym and is used as such in the text. *Apparent mortality* values cannot be added, while *relative mortality* values can, either to give aggregate parasitism for a group of parasites, or for all parasites acting on a given generation of the host.

An example of the method used in estimating the *relative parasitism* in the present study is shown in Table I. The parasites were divided into three groups: those emerging from the early larval stage, from the late larval stage, and from the pupal stage. The individual parasite species within the groups were considered as acting on the same host population. Since *relative parasitism* by the first group is calculated directly from the number of hosts in rearing that produced either adults or parasites, it is, therefore, equal to the *apparent parasitism*. *Relative parasitism* for the second group, is calculated by reducing the apparent parasitism of individual species by the aggregate parasitism of the first group; in the third group, *apparent parasitism* must be reduced by the combined action of the first two groups. Total parasitism is obtained by adding the relative parasitism of all parasite species, or the aggregate relative parasitism for the groups of parasites that acted on the host during specific phases of development. Although this method of obtaining total parasitism is somewhat different from the one advocated by Bess (1945), the results of the two methods are the same.

The action of the egg parasite, *Trichogramma minutum* Riley, was not taken into consideration in these calculations. As a result of widespread surveys, egg parasitism was found to be consistently low (less than three per cent for the whole region) and varied little from year to year[2].

Results

Table II gives the average spruce budworm population for three collections on sprayed and unsprayed plots during the years of study; data for 1954 were

[2]Personal communication by R. Martineau.

TABLE I.
Estimation of relative parasitism for individual parasite species, and of aggregate relative parasitism for groups of parasites acting in sequence

Group	Parasite species	Apparent parasitism %	Relative parasitism %	Aggregate relative parasitism %
I (early larvae)	*Apanteles fumiferanae*	13.8	13.8	18.1
	Glypta fumiferanae	4.3	4.3	
II (late larvae)	*Meteorus trachynotus*	22.2	18.2	22.5
	Phryxe pecosensis	5.3	4.3	
III (pupae)	*Itoplectis conquisitor*	2.3	1.4	11.6
	Phaeogenes hariolus	17.1	10.2	
Total			52.2	52.2

incomplete and are not included. Population levels in 1954, however, were very similar to those existing from 1955 to 1957. Although during these three years insect numbers varied somewhat between plots, they were generally sufficiently high in unsprayed plots to cause severe defoliation (from 75 to 100 per cent) of the current year's growth. In 1958, however, population levels were much lower than in preceding years and defoliation was light.

On all plots natural control factors caused populations to decline from the time of emergence in the spring to the adult stage in mid-summer, and this was reflected in a reduction in the number of insects per unit length of branch between the first, second, and third collections. Spraying took place between the first and second collections, and contributed to the reduction in population level between the first and later collections. In sprayed areas, population levels were

TABLE II.
Average population per 18-inch branch tip for sprayed and unsprayed plots for each collection from 1955 to 1958

Year of study	Collection	Spraying History*		
		Unsprayed†	Sprayed year of study	Sprayed one year previous to year of study
1955		(5)	(1)	(1)
	I	20.8	23.8	3.7
	II	6.4	1.7	3.0
	III	5.0	1.1	0.7
1956		(8)		(3)
	I	34.1		6.9
	II	13.5		3.3
	III	8.8		4.0
1957		(5)	(2)	(2)
	I	42.6	17.9	11.0
	II	4.3	3.0	6.8
	III	4.3	1.9	1.8
1958		(8)		
	I	7.3		
	II	1.5		
	III	0.3		

*Number of plots shown in brackets.
†Includes some plots sprayed two years or more prior to year of study.

TABLE III.

List of parasite species reared from spruce budworm in the Lower St. Lawrence and Gaspé between 1954 and 1958.

Hymenoptera

Braconidae:

Apanteles fumiferanae Vier.
Macrocentrus iridescens French
Meteorus trachynotus Vier.

Ichneumonidae:

Campoplex mellipes (Prov.)
Apechthis ontario (Cress.)
Glypta fumiferanae (Vier.)
Horogenes cacoeciae (Vier.)
Itoplectis conquisitor (Say)
Mesochorus sp.
Phaeogenes hariolus (Cress.)

Trichogrammatidae:

Trichogramma minutum Riley

Pteromalidae:

Amblymerus verditer (Nort.)
Coelopisthia sp.
Psychophagus omnivorus (Wlkr.)

Diptera

Metopiidae:

Agria affinis (Fall.)
Sarcophaga aldrichi Park.

Tachinidae:

Actia interrupta Curr.
Eumea caesar (Ald.)
Ceromasia auricaudata (Tns.)
Lypha setifacies (West.)
Madremya saundersii (Will.)
Nemorilla pyste (Wlk.)
Omotoma fumiferanae (Tot.)
Pseudoperichaeta erecta (Coq.)
Phryxe pecosensis (Tns.)

usually low the year following treatment, but there was little or no difference between sprayed and unsprayed plots the second year. For this reason, no distinction was made between plots sprayed two years or more prior to the year of study and unsprayed plots.

Table III gives the different species of parasites recovered from spruce budworm from 1954 to 1958 in the Lower St. Lawrence and Gaspe. *Apanteles fumiferanae* and *Glypta fumiferanae* were the most common species and were obtained from every plot each year. *Meteorus trachynotus*, *Omotoma fumiferanae*, *Itoplectis conquisitor*, *Phaeogenes hariolus*, and *Apechthis ontario* were relatively common and periodically occurred in abundance. It is noteworthy that these same species were among those most frequently recovered in northwestern Ontario (McGugan and Blais, 1959). The majority of the parasite species found in Quebec were rare, some being obtained as single specimens. Three of the species are new records, namely: *Campoplex mellipes* (Prov.), *Psychophagus omnivorus* (Wlkr.), and *Coelopisthia* sp. It is possible, however, that the species of *Campoplex* is the same as that found in the Cabonga area of Quebec by Daviault (1950) and recorded only as genus.

TABLE IV

Incidence of parasitism by *Apanteles fumiferanae* and *Glypta fumiferanae* as determined by laboratory rearings and by dissection for various plots in 1955 and 1957.

Year	Plot	No. of larvae reared	No. of larvae dissected	Percentage Parasitism			
				Laboratory rearings		Dissection	
				Apanteles	*Glypta*	*Apanteles*	*Glypta*
1955	4	233	67	4.3	3.0	8.9	3.0
	5	215	165	4.2	4.7	12.7	4.8
	7	189	100	7.4	9.5	14.0	8.0
	9	239	100	2.1	5.9	7.0	5.0
		876	432	4.3	5.6	13.4	5.3
1957	4	150	189	1.3	6.6	2.1	1.6
	11	159	85	5.7	8.1	13.0	5.9
	13	114	146	7.0	14.0	14.4	14.4
	14	138	120	12.3	16.7	22.6	16.7
		561	540	6.4	11.0	12.6	9.8

In 1955 and 1957, the incidence of parasitism by *Apanteles fumiferanae* and *Glypta fumiferanae* was determined for a number of plots by dissection of larvae collected at the same time as those kept for rearing (Table IV). The parasites were identified in the larval stage according to criteria described by Brown (1946a, 1946b). The percentage parasitism by *Glypta fumiferanae* was generally the same in the rearings as in the dissected material. In both years, however, considerably more larvae were found parasitized by *Apanteles fumiferanae* in the dissected material than through rearing. *Apanteles fumiferanae* was the first parasite species to emerge and larvae parasitized by this species do not develop beyond the fourth or fifth instar. Furthermore, the development of larvae parasitized by *Apanteles fumiferanae* is greatly retarded (McGugan, 1955), and for this reason they are perhaps more prone to being lost or accidentally destroyed through cannibalism or through handling in the course of rearing than the larger unparasitized larvae. It is possible that in the field larvae parasitized by *Apanteles fumiferanae* are also prone to be destroyed prior to the emergence of the parasite. The present data, however, would indicate that the incidence of parasitism by *Apanteles fumiferanae* in field populations was in effect greater than that obtained through rearing.

Tables V to IX present the total number of spruce budworm larvae and pupae reared, that is, the number that produced either adults or parasites, and the relative per cent parasitism by species for the various plots for each year of study. The relative per cent parasitism was calculated according to the method described above. All larvae and pupae that died in rearing through causes other than parasitism were deleted from the totals and did not figure in the calculations as it was assumed that they contained an equal proportion of parasites as those surviving these hazards. Larvae parasitized in their early development were not available to parasites which attack the later larval stages, consequently the occurrence of such larval parasites as *Meteorus trachynotus* was calculated by reducing the sample by the number that yielded *Apanteles fumiferanae* and *Glypta fumiferanae* in addition to the number that were missing or had died of unknown causes. Each year, some parasites failed to develop completely and could only be identified as Hymenoptera or Diptera; these are shown as such in the tables. The

TABLE V

Relative per cent parasitism[1] by species for various plots studied in 1954

Plot	1	2	3	4	5
Number of budworm reared	782	628	493	1,046	3,698
Apanteles fumiferanae	3.1	5.9	2.1	2.4	2.6
Glypta fumiferanae	4.3	4.2	4.1	5.8	7.3
Horogenes cacoeciae	0.6	0	0	0.8	0
Meteorus trachynotus	4.6	10.3	0.5	0	0.5
Nemorilla pyste	0	0	0	0	0.2
Phryxe pecosensis	15.2	11.5	2.3	1.3	0.7
Actia interrupta	0	1.9	0	0	1.2
Omotoma fumiferanae	3.1	1.5	2.3	1.9	2.5
Pseudoperichaeta erecta	0	0.3	0	0	0
Sarcophaga aldrichi	0	0	3.6	0	0.1
Agria affinis	0.7	2.3	1.6	0.5	0.1
Eumea caesar	3.1	4.5	0.5	0	0.9
Madremya saundersii	0	0	0	0	1.1
Itoplectis conquisitor	0.2	0	0	0	0.1
Phaeogenes hariolus	2.2	3.6	4.1	1.1	6.7
Apechthis ontario	13.3	5.0	10.5	4.0	3.3
Amblymerus verditer	1.3	0	0	0	0.2
Total parasitism	51.7	51.0	31.6	17.8	27.5

[1]See text

data in Tables V to IX indicate that the incidence of some parasite species varied between plots within years (especially in 1958), and that variations also occurred between years within plots.

Table X shows, for all plots taken together, the yearly relative per cent parasitism for each of the more common parasite species. When the per cent parasitism of an individual species is being compared from year to year for the whole

TABLE VI

Relative per cent parasitism[1] by species for the various plots studied in 1955

Plot	2	4	5	7	9	10	13
Number of budworm reared	562	724	848	640	792	384	787
Apanteies fumiferanae	9.3	4.3	4.2	7.4	2.1	13.7	14.7
Glypta fumiferanae	12.4	3.0	4.7	9.5	5.9	11.8	8.6
Horogenes cacoeciae	0	0	0	0	0.3	0	0
Meteorus trachynotus	3.4	1.7	1.3	0.9	1.7	2.9	1.0
Phryxe pecosensis	0	0	0	0	0.3	0	0
Campoplex meilipes	0	0	0	0	0	0.4	0
Actia interrupta	0	0.6	0.2	0.4	0.9	2.6	11.5
Lypha setifacies	0.3	2.0	0.2	0	1.2	0.6	0
Omotoma fumiferanae	4.0	5.6	9.3	2.3	3.0	7.6	0.9
Eumea caesar	0	0	0	0	0.3	0	0
Pseudoperichaeta erecta	0	0	0	0	0.3	0	0
Agria affinis	0	1.6	1.2	1.7	1.4	0	0.3
Itoplectis conquisitor	0.5	0.6	0	1.4	1.0	0	0
Phaeogenes hariolus	1.0	4.4	1.0	4.2	5.1	0	2.0
Apechthis ontario	0.5	0	1.2	2.8	5.5	0.7	0
Amblymerus verditer	0	0.3	0.1	0.3	0.3	0	1.1
Other Hymenoptera	0	0	0.1	1.4	1.4	0	0.4
Other Diptera	0	0	0	0	0	0	0.1
Total parasitism	31.4	24.1	23.5	32.3	30.7	40.3	40.6

[1]See Text

TABLE VII

Relative per cent parasitism[1] by species for the various plots studied in 1956

Plot	2	4	5	7	9	10	11*	12	13	15	18*
Number of budworm reared	373	629	668	725	792	860	48	724	979	820	221
Apanteles fumiferanae	4.1	10.9	3.2	7.4	3.1	13.5	14.8	3.7	12.3	7.0	12.2
Glypta fumiferanae	4.1	5.5	4.3	11.1	5.5	15.9	6.2	14.2	20.9	19.4	4.1
Meteorus trachynotus	0	0.2	0	6.4	0.4	0.5	–	0.3	0	0.7	–
Phryxe pecosensis	0.6	0	0	0.9	0.4	0	–	0	0.3	0.4	–
Actia interrupta	0	0.8	0.6	0.6	0	0.2	–	0	0	0	–
Lypha setifacies	0	0.8	0	0	0	0	–	0	0	0	–
Omotoma fumiferanae	1.3	0.8	1.8	2.1	3.7	3.4	–	8.1	1.0	2.5	–
Eumea caesar	0	0	0	0.5	0	0	–	0	0	1.1	–
Agria affinis	0	0	0	0	0	0	–	0.3	0	0	–
Itoplectis conquisitor	0	1.1	1.3	1.2	1.7	0.2	–	0	0.2	0.5	–
Phaeogenes hariolus	0	0	0	5.7	0.7	1.3	–	1.3	1.1	1.4	–
Apechthis ontario	0	0	0.3	0.8	0.3	0	–	0	0	0	–
Coelopisthia sp.	0	0	0	0	0	0	–	0	0.2	0	–
Other Hymenoptera	0	0	0.4	1.2	1.7	0.7	–	0.3	0	0	–
Other Diptera	0.5	0.5	0	0.4	0.8	0.5	–	1.1	0.4	0.5	–
Total parasitism	10.6	20.6	11.9	38.3	18.3	36.2	–	29.3	36.4	33.5	–

[1]See text.
*Only early larval stage was collected for recovery of *Apanteles* and *Glypta*.

region, minor fluctuations have to be disregarded, because of the intra-plot variability with respect to the relative abundance of some parasite species in certain years. However, pronounced trends may be considered as reflecting a general situation. The data in Table X indicate that *Apanteles fumiferanae* was least abundant in 1954, maintained a fairly high level from 1955 to 1957, and showed a slight increase in 1958. For the first four years of study, *Glypta fumiferanae* was consistently among the two most common species encountered. In the last year of the outbreak, however, this species was fifth in order of relative abundance. *Meteorus trachynotus* and *Itoplectis conquisitor* were quite rare

TABLE VIII

Relative per cent parasitism[1] by species for various plots studied in 1957

Plot	4	5	6	7	8	10	11	13	14
Number of budworm reared	224	342	180	434	373	582	340	511	462
Apanteles fumiferanae	1.3	6.0	9.4	7.7	3.1	14.6	5.7	7.0	12.3
Glypta fumiferanae	6.6	3.0	2.4	9.8	3.1	15.3	8.1	14.0	16.7
Horogenes cacoeciae	0	0	0.9	0	0.9	0	0	0	0
Meteorus trachynotus	0	1.6	0	1.2	1.0	0.3	0	0.5	0
Phryxe pecosensis	0	0	0	1.0	1.8	0.8	0	0	0
Mesochorus sp.	0	0	0	0	0	0	0	0.5	0
Actia interrupta	0	0	0	0	0	0	1.9	0	0
Omotoma fumiferanae	0	0	0	6.3	1.1	2.3	0.9	1.9	0.8
Ceromasia auricaudata	0	0	0	0.4	0	0	0	0	0
Agria affinis	0	1.1	0	0	0	0	0	0	0
Itoplectis conquisitor	0	0	0	0	1.1	0	0	0	0
Phaeogenes hariolus	0	9.6	8.3	24.5	15.6	16.4	7.6	0.4	2.3
Apechthis ontario	0	1.1	0	0.8	0	0.6	0	0	0
Other Hymenoptara	0	0.7	4.1	1.6	3.6	1.2	3.2	0	0.4
Other Diptera	0	1.1	4.1	1.6	3.6	0.3	2.2	0	0
Total parasitism	7.9	24.2	29.2	54.9	34.9	51.8	29.6	24.3	32.5

[1]See text.

TABLE IX
Relative per cent parasitism[1] by species for various plots studied in 1958

Plot	5	7	8	10	11	13	16	17
Number of budworm reared	146	307	425	471	309	376	356	384
Apanteles fumiferanae	13.8	9.6	5.6	11.2	19.4	12.9	20.0	5.5
Glypta fumiferanae	4.3	0.6	2.5	7.0	2.8	14.4	1.8	1.1
Horogenes cacoeciae	0	0	0	0	0.9	0	0	0.8
Meteorus trachynotus	18.2	26.4	5.6	2.8	0.7	23.2	35.4	3.4
Phryxe pecosensis	4.3	0	6.1	0.4	0	0.4	0.5	1.1
Macrocentrus iridescens	0	0	0	1.1	0	0	0	0
Actia interrupta	2.5	6.0	0	0	2.0	1.3	0	0
Lypha setifacies	0	0	0.5	0	0	0	0.6	0
Omotoma fumiferanae	8.6	4.8	3.5	4.4	0	0.4	2.0	1.5
Sarcophaga aldrichi	3.7	0	0	3.1	0	9.5	0	4.9
Agria affinis	0	0	5.1	0	0	0	0	0
Itoplectis conquisitor	3.7	0	5.1	3.1	24.7	0	2.9	34.6
Phaeogenes hariolus	0	10.4	12.2	17.5	4.4	0	2.7	5.9
Apechthis ontario	3.7	0	3.1	4.8	4.4	9.5	1.5	4.2
Psychophagus omnivorus	0	0	3.1	0	0	0	0	0.8
Amblymerus verditer	0	0	3.1	1.7	0	9.5	0	0
Other Hymenoptera	11.2	0.7	3.1	0	0	0	0	2.5
Other Diptera	3.7	0	0	3.1	24.7	0	0	0.8
Total parasitism	77.7	58.5	58.6	60.2	84.0	81.1	67.4	67.1

[1]See text.

from 1954 to 1957, but in the last year of the outbreak showed a spectacular increase, and accounted for the greatest percentage mortality through parasitism in 1958. The average parasitism by *Omotoma fumiferanae* varied little during the five years of study. *Apechthis ontario* was recovered in greatest abundance in 1954, became rare in 1956 and 1957, and showed an increase in 1958. *Phaeogenes hariolus*, although fairly common in the first three years of study, showed a considerable increase in 1957 when it was the most abundant species; it continued to be abundant in 1958.

Although the effect of aerial spraying on spruce budworm parasites was not a primary objective of these studies, some information on this aspect was obtained. As mentioned earlier, *Apanteles fumiferanae* and *Glypta fumiferanae* were the two most common parasites recorded in these studies, and with the exception of *Horogenes cacoeciae* (a rare parasite in the study area), they are the only species that overwinter in the spruce budworm. *Apanteles fumiferanae* and *Glypta fumiferanae* usually did not emerge from host larvae until shortly after aerial spraying had been completed. Collections for estimating the incidence of *Apanteles fumiferanae* and *Glypta fumiferanae* were always made prior to the application of the insecticide, consequently it was not until the year following

TABLE X
Yearly relative per cent parasitism for each of the more common parasite species for all plots

	1954	1955	1956	1957	1958
Apanteles fumiferanae	2.8	7.8	8.1	7.3	11.7
Glypta fumiferanae	6.2	7.8	10.9	8.6	4.6
Meteorus trachynotus	2.8	1.8	1.5	0.8	13.6
Omotoma fumiferanae	2.3	5.0	2.8	2.7	2.8
Itoplectis conquisitor	0.2	0.9	0.7	0.9	14.3
Apechthis ontario	5.7	2.5	0.4	0.6	3.3
Phaeogenes hariolus	4.6	2.8	1.9	8.8	7.2

TABLE XI

Average per cent parasitism by *Apanteles fumiferanae* and *Glypta fumiferanae* for plots studied one year after spraying, and for unsprayed plots studied the same year

Year studied	No. of plots sprayed previous year	No. of unsprayed plots	Av. % parasitism sprayed plots		Av. % parasitism unsprayed plots	
			Apanteles	*Glypta*	*Apanteles*	*Glypta*
1955	1	6	4.3	3.0	8.4	8.6
1955	3	8	10.8	4.4	7.6	12.0
1957	2	7	6.2	2.7	7.6	10.1
All years	6	21	7.6	3.5	7.8	10.6

treatment that any effect of spraying on these species could be estimated. Between 1955 and 1957, collections were made from a total of six plots where spraying had taken place the preceding year. The average per cent parasitism by *Apanteles fumiferanae* and *Glypta fumiferanae* for sprayed and unsprayed plots is given by years in Table XI. Although the incidence of parasitism by *Apanteles fumiferanae* was greater in the unsprayed than in the one sprayed plot in 1955, parasitism by this species showed no significant difference between unsprayed and sprayed plots in 1956 and 1957. The incidence of parasitism by *Glypta fumiferanae* was at least three times as great in unsprayed as in sprayed plots each year of study. This would indicate that spraying had little or no effect on *Apanteles fumiferanae* but that *Glypta fumiferanae* suffered to some degree. The results obtained by Macdonald (1959) concerning the effects of the aerial application of DDT on *Apanteles fumiferanae* and *Glypta fumiferanae* in New Brunswick were somewhat different. He found that *Apanteles fumiferanae* tended to increase in sprayed areas in the year of spray application as well as in the year following, while *Glypta fumiferanae* did not appear to be affected by the sprays.

Most other parasite species were not present in the host at the time of spraying. Their complete life history is not known and it is difficult to determine their vulnerability to the insecticide. There is no evidence from the present data that the other parasite species were affected adversely.

Total mortality due to the action of insect parasites was calculated for each plot and each year according to the method described earlier. In 1955, 1956, and 1957 a few plots were sprayed during the year of study or the year preceding. Although the degree of parasitism was generally somewhat less in sprayed plots (possibly owing to the adverse effects of the sprays on *Glypta fumiferanae*) the sample was inadequate to show that the decrease in parasitism was attributable to the insecticide. Therefore, when the yearly average per cent mortality for all plots was calculated, sprayed plots were included with the unsprayed ones.

Mortality through the action of parasites varied somewhat between plots within years. When the average annual per cent mortality resulting from the action of insect parasites for all plots is compared, there is very little difference between the first four years of study. In 1958, however, the parasitism increased tremendously throughout the region, and was double that of any of the four previous years. This situation was the result of the increased action of a number of parasite species, but mostly that of *Meteorus trachynotus* and *Itoplectis conquisitor*. It is significant that *Glypta fumiferanae* was the only species that exhibited a noticeable decline in 1958.

TABLE XII

Locality, spraying history, and total per cent mortality due to insect parasites for each plot and year of investigation

Plot No.	Locality	Spraying history	Annual Per Cent Parasitism				
			1954	1955	1956	1957	1958
1	Rioux Seignory	Unsprayed	51.7				
2	Rimouski River	1955	51.0	31.4	10.6		
3	Plate River	Unsprayed	31.6				
4	Metis Lake	1954, 1957	17.8	24.1	20.6	7.9	
5	Metis Lake	Unsprayed	27.5	23.5	11.9	24.2	77.7
6	Metis Lake	1956				29.2	
7	Matapedia Lake	Unsprayed		32.3	38.3	54.9	58.5
8	Matapedia Lake	1956				34.9	58.6
9	Matane River	Unsprayed		30.7	18.3		
10	Harriman Lake	Unsprayed		40.3	36.2	51.8	60.2
11	Grand Cascapedia River	1955			-(*)	29.6	84.0
12	Berry Mountain Depot	Unsprayed			29.3		
13	Pabos River	Unsprayed		40.6	36.4	24.3	81.1
14	Pabos River	1957				32.5	
15	Percé	Unsprayed			33.5		
16	Patapedia River	Unsprayed					67.4
17	Nouvelle River	1955					67.1
18	Grand Cascapedia River	1955			-(*)		
	Average for all plots		31.4	31.1	27.8	34.7	68.1

*Only collections I and II made.

Discussion and Conclusions

The similarity between the spruce budworm parasite complex in outbreaks reported previously in eastern North America and the present study is striking. Dowden *et al.* (1950) in New York, Jaynes and Drooz (1952) in Maine, Macdonald (1959) in New Brunswick, McGugan and Blais (1959) in northwestern Ontario, have observed that *Apanteles fumiferanae* and *Glypta fumiferanae* were the most common parasites in the earlier years of these respective outbreaks. These same authors record that the increase in parasitism by *Meteorus trachynotus* was very noticeable in the last year of the outbreaks. These observations agree with those made in the Lower St. Lawrence and Gaspe Peninsula. However, there were many differences respecting the parasite complex in each of these outbreaks. The relative abundance of certain parasite species in both the earlier years and later years of these other outbreaks differed markedly. These differences were evident even between outbreaks that occurred almost simultaneously and which were more or less continuous geographically, such as the New York and Maine outbreaks, and particularly the New Brunswick and the Quebec outbreaks. In the latter case for instance, *Glypta fumiferanae* was relatively much more abundant in Quebec than in New Brunswick for many years; in the last year of the infestation, *Horogenes cacoeciae* showed a marked increase in New Brunswick but was almost absent in Quebec, while *Itoplectis conquisitor* and other pupal parasites were more abundant in Quebec than in New Brunswick. Such differences are understandable, especially in the case of the non-specific parasite species that may have two or more generations in a year and require alternate hosts. The presence and the relative abundance of alternate hosts are undoubtedly affected by variations in such factors as topography, climate, and forest composition. The aggregate parasitism in the northeastern States was generally higher than that observed in Ontario, Quebec, or New Brunswick and

in addition, a number of species not present or rare in Canada such as *Dicladocerus* sp. and *Lestodiplosis* sp. were fairly common in the northeastern States. The greater abundance of parasite species in Maine and New York may be due to the presence of certain alternate hosts which are absent in the boreal forest of eastern Canada, and may explain the short duration of the recent spruce budworm outbreaks in the northeastern States compared with the more prolonged and destructive outbreaks in Canada.

The increase in parasitism during the last year of the outbreak in the Lower St. Lawrence and Gaspe Peninsula appeared to be a consequence rather than the cause of the decline in budworm populations. The unfavourable summer weather conditions in 1956 and 1957 initiated the decline (Blais, 1958a, 1958b), and the spraying operations contributed to a further lowering of spruce budworm population levels. Notwithstanding the greatly reduced insect numbers in 1957, parasites maintained a fairly even level with that of previous years. By 1958, however, spruce budworm numbers were depressed to a point where insect parasites, along with other natural control factors, could bring about the final collapse of the outbreak.

Summary

Parasite investigations were carried out between 1954 and 1958 in a spruce budworm outbreak in the Lower St. Lawrence and Gaspe Peninsula. The relative abundance of a number of parasite species varied between localities within years and between years. Most of the 25 parasite species encountered were rare or occasional. In the first four years of investigation *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) were the most common species recorded. In the last year of the outbreak *Meteorus trachynotus* Vier., and *Itoplectis conquisitor* (Say) showed spectacular increases. The aerial application of DDT over a period of five years did not appear to affect the parasite complex with the possible exception of *Glypta* which was less abundant in sprayed plots. The average yearly mortality through insect parasites for all the plots studied maintained itself at a fairly constant level from 1954 to 1957, but increased considerably in the last year of the outbreak. The similarities and differences between the parasite complex in recent spruce budworm epidemics in eastern North America are briefly discussed. The increase in the incidence of mortality through insect parasites appears to be the result of a general decline in spruce budworm numbers as a consequence of unfavourable weather conditions. Parasites, however, were an important factor contributing to the final collapse of the outbreak.

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Immature Stages of *Chaoborus borealis* Cook (Diptera: Culicidae)

By B. C. Smith
Entomology Research Institute for Biological Control, Research Branch
Canada Department of Agriculture, Belleville, Ontario

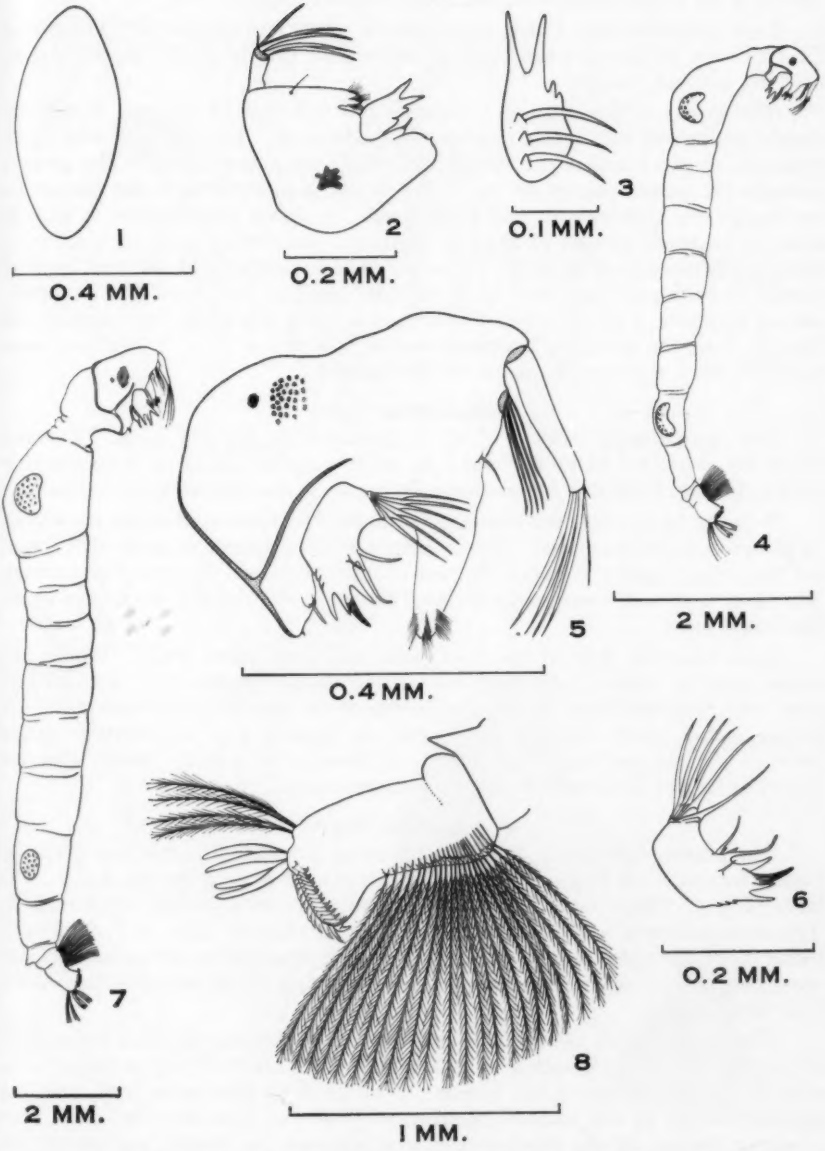
The immature stages and adults of *Chaoborus borealis* Cook were collected near Churchill, Manitoba, in 1949 and 1950 in investigations on the natural control of biting flies (James, 1953; James and Smith, 1958). Cook (1956) described the adult and the fourth-instar larva in his revision of the Nearctic Chaoborinae, and noted the similarity between the fourth-instar larva and that of *C. flavicans* (Mg.). This paper contains descriptions of the egg, the first-, second-, and fourth-instar larvae, and the pupa of *C. borealis*.

Egg

The egg (Fig. 1) is oval, 0.5 mm. long, and 0.2 mm. wide. It is amber in colour and has no prominent surface markings. The eggs are laid in masses that float on the water surface, each mass containing approximately 60 eggs. The eggs are bound together by a gelatinous substance in which are embedded numerous setae from the abdomen of the female.

First-Instar Larva

The first-instar larva is approximately 2.5 mm. long. The cuticle is transparent. The head (Fig. 2) tapers from the posterior margin to where the antennae are attached. Each antenna has a single, stout segment bearing four long and two short setae at its end. One of the short setae is approximately half as long as the long setae, whereas the other is much shorter. Two setae, one on each side, are situated posterior to the antennae. The labrum is a fingerlike lobe



Figs. 1-8. *C. borealis*. 1, Outline of egg. 2 and 3. First-instar larva. 2, head; 3, left mandible, medial view. 4-6. Second-instar larva. 5, head; 6, right mandible, lateral view. 7-11. Fourth-instar larva. 8, anal segment.

with a number of setae at its distal end. The maxillary palpi are posterior to the mandibles. Each stipes forms a broad plate with a seta near its ventral margin. The eyes are deeply pigmented and have irregular margins.

Each mandible (Fig. 3) has four teeth, two long and two short. Three long setae, or rays, each with a short seta at its base, are present on the medial surface near the anterior margin.

The thorax is unjointed and contains the first pair of air sacs, which are deeply pigmented and visible through the body wall. The first five abdominal segments are thicker than the remainder, which taper posteriorly. The seventh contains the second pair of air sacs. Colourless, compound setae are present on the thorax and abdomen as well as the head. A dorsal protuberance is present near the posterior margin of the anal segment. According to Cook (*loc. cit.*), this protuberance is of the ninth segment. The appendages of the anal segment consist of four pectinate setae, four elongate papillae, two hook-like processes, one on each side, a double row of processes on each side extending laterally and dorsally from the hook-like processes, and an anal fan of 15 to 22 pectinate setae that arise from the ventral margin of the segment.

Second-Instar Larva

The second-instar larva (Fig. 4) is approximately 4.2 mm. long. The anal fan is composed of 18 to 22 setae. In other respects the larva is structurally similar to that of the first instar except for some of the characters of the head.

A group of 10 elongated setae arise from the ventral margin of the head (Fig. 5) posterior to the antennae. Two shorter setae are present as in the first instar, but they arise midway between the base of the labrum and the group of 10 setae. The hinge lines of the mandibles lie more nearly in a horizontal plane than in the first-instar larva.

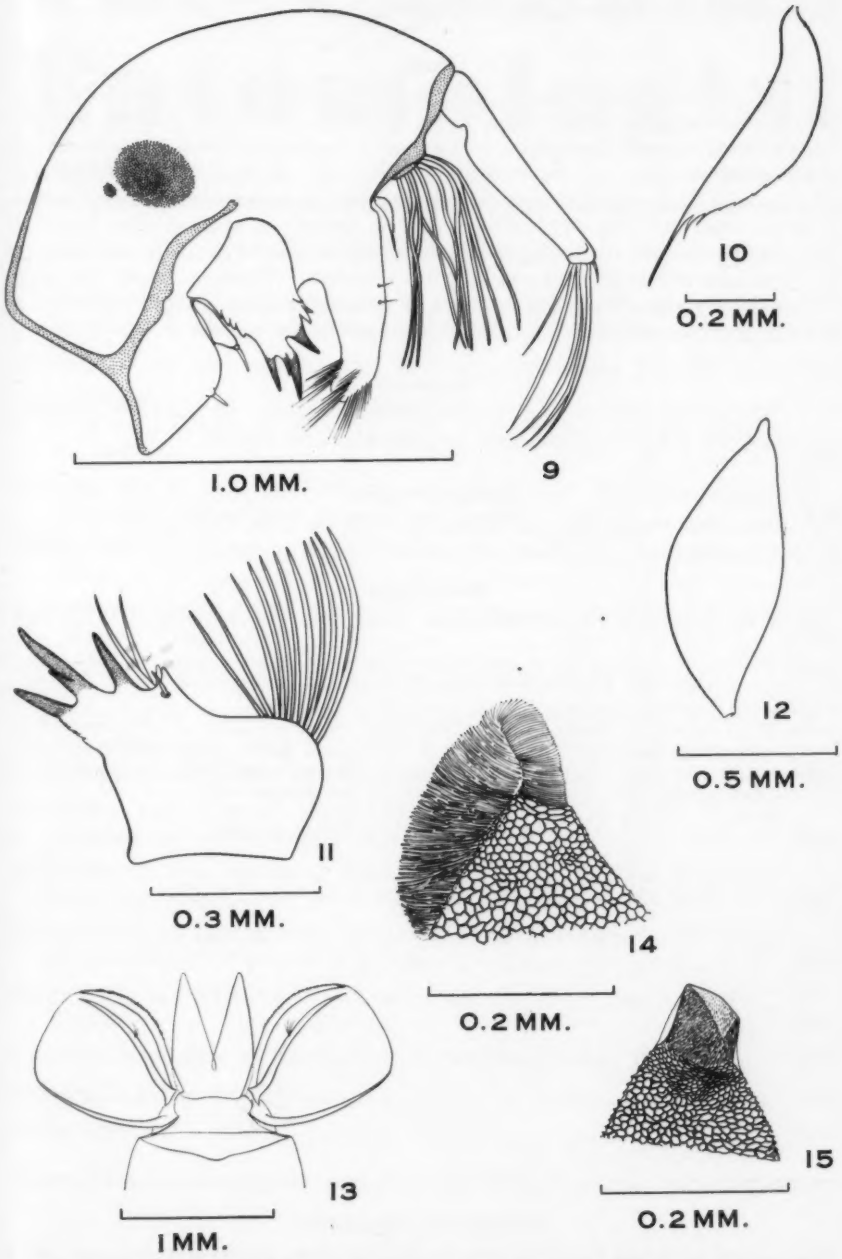
Each mandible (Fig. 6) has three major and three minor teeth. The middle major tooth is bilobed, the main lobe being deeply pigmented. Six elongate setae arise ventrally from the anterior corner of the mandible and form a fan. A group of two short and two long setae are present near the ventral margin between the fan and the major teeth. A short, stout process arises from the lateral surface of the mandible near the ventral margin.

Fourth-Instar Larva

The present description of the fourth-instar larva supplements that given by Cook (*loc. cit.*). Both larvae and exuviae were used to describe this stage. The larva (Fig. 7) differs from that of the second instar in a number of characters. The average length is 10.90 mm. and ranges from 10.00 to 12.00 mm., the female being slightly longer than the male. The anal papillae of the last abdominal segment (Fig. 8) are shorter in proportion to the length of the segment than in the first two instars.

The head (Fig. 9) has a pair of leaf-like appendages one of which is shown in Figure 10. In the male each is approximately seven times as long as wide. This ratio is slightly smaller in the female. Two pairs of setae arise from near the anterior margin of the labrum approximately halfway from its distal end. The posterior margin of the head is deeply pigmented. A deeply pigmented line extends from the occipital margin to a point below each compound eye. The simple eyes are small and are posterior to the compound eyes.

Each mandible (Fig. 11) has four or five minor teeth and three deeply pigmented major teeth, the middle one of which is bilobed. There are 11 setae in the female fan and 12 in the male. The group of four setae between the major



Figs. 9-15. *C. borealis*. 9-11. Fourth-instar larvae. 9. head; 10, leaf-like appendage; 11, left mandible, lateral view. 12-15: Pupa. 12, right respiratory horn; 13, anal paddles of male, ventral view; 14, proximal end of respiratory horn; 15, distal end of respiratory horn.

teeth and the fan are similar to those of the second instar except that the longer setae are relatively longer than the shorter ones.

Pupa

The pupa appears similar in form to that of *Chaoborus albipes* Johannsen (1934). It varies in colour from yellow-green in the newly formed to light brown shortly before emergence. The most conspicuous external structures are the respiratory horns of the thorax (Fig. 12) and the anal paddles (Fig. 13). The surfaces of the horns are reticulated and each horn joins the tracheal system at its proximal end (Fig. 14) and has a narrow opening at its distal end (Fig. 15). Each paddle consists of a broad, membranous area bordered medially and laterally by stout ribs and supported centrally by a midrib. There are tooth-like projections along the distal three-quarters of the medial rib. A plumose seta is situated approximately halfway along the length of the midrib.

Summary

The egg, the first-, second-, and fourth-instar larvae, and pupa of *Chaoborus borealis* Cook (Diptera: Culicidae) are described with figures.

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